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Effects of glacial influence on trophic function of benthic fauna in tropical high-Andean streams

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Certifico que la Tesis de la maestría en Biología de la Conservación del candidato Patricio Javier Andino Guarderas ha sido concluida de conformidad con las normas establecidas; por lo tanto, puede ser presentada para la calificación correspondiente.

Verónica Crespo-Pérez, Ph.D.

Directora de la Tesis

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1. RESUMEN

Las características de arroyos alimentados por glaciares afectan a las comunidades de macroinvertebrados, tanto en zonas templadas como tropicales. Las cadenas alimenticias de los arroyos de origen glaciar en los Alpes, presentan características específicas. Sin embargo, no se sabe nada acerca de la organización de las redes tróficas en los arroyos alimentados por glaciares tropicales. Comprender las conexiones entre diferentes niveles de organización del ecosistema, puede ayudar a desarrollar un marco teórico más coherente para predecir las consecuencias ecológicas de Cambio Climático (CC). Mejorando la comprensión acerca de las repercusiones del CC sobre la capacidad de recuperación (resiliencia) ecológica, y el futuro uso de este conocimiento para el manejo de la biodiversidad afectada por el retroceso glaciar. Ejecutado en las faldas del volcán nevado Antisana, los sitios de estudio fueron designados para cubrir un gradiente de Influencia Glaciar (IG en adelante). Basado en el efecto amortiguador de otros tipos de arroyos sobre los de origen glaciar. Clasificados utilizando un Índice de Influencia Glaciar modificado, que integra las variables ambientales particulares de arroyos alimentados por glaciares tropicales. Los resultados indican que la abundancia de los gremios alimenticios se relacionó negativamente con la IG, mientras que la riqueza los Grupos Funcionales Alimenticios (GFA) fue menos afectada. Se halló redundancia funcional en niveles intermedios de IG, ya que los nuevos colonizadores poseen rasgos similares a los taxones ya presentes en niveles más altos. Y así, los procesos de filtración de nicho se originan por la severidad ambiental causada por la IG. Los hábitos alimenticios más especializados se distribuyen en corrientes más estables, a medida que luchan para evitar desequilibrios entre la oferta y la demanda. En ambientes severos, los hábitos generalistas-oportunistas parecen prevalecer sobre la especialización de una sola fuente de alimento; permitiéndoles habitar un rango ambiental más amplio. La Descomposición de Materia

Orgánica Gruesa (DMOG) sigue una débil relación acampanada con la IG, indicando la dominancia de los efectos ambientales abióticos sobre la función de descomposición del ecosistema. Este estudio indica que la dinámica de la materia orgánica, en los arroyos alimentados por glaciares tropicales andinos, sostiene una baja producción autóctona, bajo ingreso y retención de materia alóctona; y procesa constantemente materia orgánica mediante abrasión física. Generando cambios en la abundancia de los GFA de macroinvertebrados, a medida que el proceso de filtrado de nichos tiene lugar a lo largo del gradiente de IG, mientras cada grupo trata de evitar desequilibrios de oferta y demanda de recursos.

Palabras clave: Andes, influencia glaciar, alimento, grupos alimenticios, descomposición, perturbación, nicho.

2. ABSTRACT

Glacial-fed stream features affect macroinvertebrate communities in both temperate and tropical streams. Alpine glacier-fed stream food chain present specific features, yet nothing is known about the organization of trophic webs in tropical glacier fed streams. Understanding the connections between different levels of ecosystem organization, can help develop a more coherent theoretical framework to predict the ecological consequences of Climate Change (CC). Enhancing our understanding of CC repercussions over ecological resilience, and the future use of this knowledge on the management of biodiversity affected by glacial retreat. Carried out at the foothills of the snowcapped Antisana volcano, sites for this study were chosen to cover a gradient of Glacier Influence (hereafter GI). Based on the diminishing GI effect of non-glacier fed over glacier fed streams. And classified using a modified Glaciality Index, that integrated the distinctive environmental variables of tropical glacier fed streams. Results indicate that feeding guild abundance was negatively related with GI, while Functional Feeding Group (FFG) richness was less affected. Functional redundancy was found at intermediate levels of GI, as new colonizers possess similar traits to taxa already present at higher levels. And so, niche filtering processes take place due to environmental harshness caused by GI. More specialized feeding habits are distributed towards more stable streams as they struggle to avoid imbalances between the supply and the demand of resources. While, in severe environments, opportunistic generalist habits seem to prevail over specialization on a single food resource; allowing them to inhabit a wider range of environments. Coarse Organic Matter Decomposition (COMD) follows a weak humped-shaped relationship with glacial influence that reflects the overriding abiotic environment effects over decomposition ecosystem function. This study indicates that organic matter dynamics in tropical andean glacier fed streams bare low autochthonous production, low

allochthonous input and retention, and constantly processing organic matter by physical abrasion. Generating shifts in macroinvertebrate FFG abundance, as niche filtering processes take place along the GI gradient, attempting to avoid supply-demand imbalances.

Key words: Andes, glacier influence, food, feeding groups, decomposition, disturbance, niche.

3. INTRODUCTION

Tropical glacier-fed streams are unique ecosystems, located in the Northern Andes, East Africa and Indonesia; and have, to date, been poorly studied (Vie 2010; Jacobsen et al. 2010; Jacobsen & Dangles 2012). These streams differ from those in temperate regions mainly because ablation of the glaciers occurs all year round in the tropics due to the lack of seasonality (Favier et al. 2008). This causes flow rates to vary daily, due to daytime thawing and nighttime freezing (Milner et al. 2009). Recently, knowledge about the ecology of streams that originate from tropical glaciers has increased, especially regarding the assembly of communities and their dynamics along altitudinal and Glacier Influence (hereafter GI) gradients (Jacobsen et al. 2010; Kuhn et al. 2011; Jacobsen et al. 2014).

Glacial features affect macroinvertebrate communities; for example, glacier size affects melting dynamics and therefore, the longitudinal patterns of stream conditions, which also affect communities composition (Castella et al. 2001). Species richness was found to increase with decreasing GI, while the percentage of Chironomidae individuals (Diptera) has been found to drastically decrease (Jacobsen et al. 2010). In the Andes, Podonominae (Chironomidae) are abundant close to the glacier, becoming less common downstream as GI decreases (Jacobsen et al. 2010). In a meta-analysis of glacial streams worldwide Jacobsen & Dangles (2012) showed that GI (combining the extent of the glacier and its distance to the study site) explained much of the variability in the richness of local taxa, following a pattern of lower richness at higher levels of GI. Therefore, GI clearly represents a stress or severity gradient and constitutes a natural disturbance to communities. However, new results indicate that species richness is maximized under intermediate glacial contribution (Jacobsen et al. 2012). This unprecedented discovery in river ecology, possibly supports the "intermediate

disturbance hypothesis" (Connell 1978) as well as the “Benign-Harsh Concept” (Menge & Sutherland 1976; Peckarsky 1983). Intermediate disturbance hypothesis states that local species diversity is maximized when ecological disturbance is neither too rare nor too frequent (Connell 1978). The Benign-Harsh Concept states that, under physically benign conditions communities would be influenced by biotic interactions, whereas in harsh environments biotic interactions would have a negligible influence on community structure (Millner et al. 2001). Nevertheless, little importance has been given to glacial streams in terms of biodiversity and conservation, probably because of their typically overall low diversity (Milner et al. 2009).

Some aquatic insects are known to change their diet in their different instars, i.e. ontogenetic shifts, (Crosby 1975; Fuller & Stewart 1979) or changing food availability (Richardson & Gaufin 1971; Lechleitner & Kondratieff 1983). Feeding habits are tied to the consumer’s food source, trophic shifting and generalism can distort relative Functional Feeding Groups (FFG) biomasses. Hence, assumptions of an organism’s FFG based solely on published classifications (e.g., Merritt & Cummins 1996) may refute the River Continuum Concept (RCC) predictions (Plague & Wallace 1998). Trophic basis of tropical macroinvertebrates has been studied, mostly by published classification assumptions (Davies et al. 2008). Overlooking species-specific functional plasticity of invertebrates may result in a misconception of invertebrate community structure. It also may lead to mistakes on predicting the effects of environmental stress on the structure of invertebrate communities (Dangles 2002), especially for less studied feeding groups in high-Andean streams (Tomanova et al. 2006; Tomanova et al. 2007; Tomanova et al. 2008).

The RCC predicts that the continuous gradient (upstream to downstream) of physical conditions, mainly related to stream size (e.g., width, discharge), affects the type and availability of food resources; which in turn, and produce a shift in the relative abundance of

FFG of macroinvertebrate communities (Vannote et al. 1980; Ward 1992; Wallace et al. 1995; Angradi 1996). Frequency of biological trait-based groups along an alpine glaciality gradient revealed the dominance of versatile resistant/resilient traits, as glacier harshness does not allow macroinvertebrate communities to develop alternative trait sets (Ilg & Castella 2006). According to Uehlinger et al. (2010) most studies have focused on benthic invertebrates and largely ignored the energy base of alpine glacier-fed streams (e.g., Burgherr 2000; Castella et al. 2001; Robinson et al. 2001; Brown et al. 2006). Increased knowledge about trophic relationships, food webs and ecological processes in glacier-fed streams in temperate regions has been obtained over the last decade (Lavandier & Décamps 1983; Zah & Uehlinger 2001; Zah et al. 2001; Füreder et al. 2001; Brittain & Milner 2001; Füreder et al. 2003; Clitherow et al. 2013). Based on May's (1972, 1973) criterion of community stability, food webs are characterized by the number of species (S), the number of links between species (L), chain length (number of trophic links between primary producers and the top predator in an ecosystem) and link density (L_D) (L_D=L/S) as a measure of connectivity (Vander Zanden et al. 1999; Ulanowicz 2008; Jennings 2008). It is known that higher L_D decreases connectivity (ratio between actual interactions and possible interactions in a food web) (Berryman 1993). Both, physiognomic simplicity environments, and energetic constraints (the number of trophic levels is limited by the ecosystem's available energy) shortens food chain length (Briand & Cohen 1987; Jenkins 1992). According with this information, alpine glacier-fed stream food webs present specific features (e.g., Brown et al. 2011) such as low taxa richness, high connectivity between taxa and a short average food chain length (Clitherow et al. 2013). To our knowledge, nothing is known about the organization of trophic food webs in tropical glacier fed streams.

Ecosystem processes like litter decomposition rates, increase with the relative abundance of the most efficient shredders (Dangles & Malmqvist 2004; Encalada et al. 2010; Dangles et al. 2011). Dangles et al. (2011) found that observed biodiversity-ecosystem function patterns fit those predicted by a linear model that described litter decomposition rates as a function of increased shredder richness and the relative abundance of the most efficient shredders. In the south-eastern Swiss Alpine glacier-fed streams that differed physically and contained different benthic communities, leaf breakdown rates and associated fungal properties varied widely among sites, reflecting site-specific differences in habitat characteristics and in macroinvertebrate and fungal composition (Robinson et al. 1998).

Tropical Andean glaciers are retreating rapidly (Francou & Coudrain 2005; Bradley et al. 2006; Ceballos et al. 2006; Chevallier et al. 2011; Condom et al. 2012; Rabatel et al. 2013), with profound effects on flow and environmental conditions in glacier-fed streams (Hagg et al. 2007). According to Woodward et al. (2012), most Climate Change (CC) studies have focused on individuals or populations, rather than on the higher levels of organization (i.e. communities, food webs, ecosystems). Understanding the connections between these different levels, which are all ultimately based on individuals, can help develop a more coherent theoretical framework based on metabolic scaling, foraging theory and ecological stoichiometry, to predict the ecological consequences of CC (Woodward et al. 2012). Quantifying spatial variation in benthic assemblages may help us foresee possible consequences of glacial retreat on biodiversity (Kuhn et al. 2011). Instead of directly assessing CC, we evaluate the effects of a phenomenon that is deeply affected by CC itself, ie glacial melting. Indeed, there is uncertainty about how it will affect biodiversity in tropical glacial streams, and which species could be lost if small equatorial glaciers completely

disappear (Brown et al. 2007; Jacobsen et al. 2012). There is even more uncertainty on the impact over trophic relations and ecosystem function.

This study attempts to provide some pioneering information on trophic relations between species and their primary food resources in small streams along a gradient of GI in a tropical catchment in the high Andes of Ecuador. Specifically we aimed to: 1) search for general relationships between GI and quantities of primary food sources (detritus and periphyton); 2) determine the composition of the diet (i.e. FFG affiliation) of the most abundant macroinvertebrate taxa; 3) elucidate the relationship between distribution patterns and metrics of macroinvertebrate feeding assemblages and the glaciality gradient, 4) test the importance of quantities of food sources for the distribution patterns of macroinvertebrate feeding guilds and 5) experimentally determine coarse organic matter decomposition (COMD) rates along the glacial influence gradient and test how these relate to specific environmental factors and macroinvertebrate assemblages. The present space-for-time substitution study will contribute to the understanding of the possible future consequences of increased glacier loss. Knowledge about the effect of species loss on community structure and functioning in streams is essential for designing management strategies to mitigate climate change effects on water resources.

4. MATERIALS AND METHODS

4.1. Study area

This study was carried out at 17 sites located in the foothills of the snowcapped Antisana volcano, at the Eastern side of the Ecuadorian Andes. Subalpine and alpine life zones, as well as limestone eroded areas caused by glacial retreat, cover the lower and upper Andean highlands (Holdridge 1967). Water draining the Antisana area serves more than 450,000 people in the south of the city of Quito. In the coming years, this service is expected to drive 1700 l/s of water and 9.5 MW of energy to the city (EPMAPS 2013). The sampling sites were located on the lower parts of the western slopes of the Antisana (Fig. 1), between 4040 and 4200 m.a.s.l. They cover a gradient of Glacial Influence (GI) and were named according to their source: glacier-fed (G), spring-fed (S), and superficial drainage (D). Stream junctions were named according to their source, i.e. GS for the junction between a glacier fed and a spring, GSD when a GS stream joins a superficial drainage and GSDGD if the last junction joins a junction between a glacier fed and a superficial drainage stream. This classification was designed to focus on the diminishing glacier influence effect of non-glacier fed over glacier fed streams. All sites were located close to each other within a small area of approximately 1.82 km^2. The farthest points (G1 and GSDSGDSS1) were located 3.13 km from each other.

4.2. Environmental variables

The abiotic environment of each site was characterized by measurements of physicochemical variables such as flow, conductivity, pH, temperature, and dissolved oxygen (both concentration and percentage of saturation). These were obtained using WTW portable meter series (WTW GmbH, Xilem Inc. Munich, Germany). Turbidity was assessed with a TN-100 EUTECH Turbidimeter. Current velocity and discharge were measured twice at each site at

the end of our field work during morning ‘base flow’ by means of dilution gauging (White 1978). A bucket of with known amount of dissolved salt (volume and conductivity) was added at the upstream end of the 20- to 25-m stream reach. We measured conductivity every 5 or 10 s at the downstream end of the reach. Current velocity was calculated as the time elapsed for half of the salt to pass through the stream reach divided by the length of the reach. Discharge (Q) was calculated from these same measurements with the formula: $Q = VC/A$, where V is the volume of salt water in the bucket, C is the conductivity of the salt water in the bucket and A is the integrated area beneath the curve from the conductivity versus time plot (Jacobsen et al. 2010).

To quantify the physical stability of the stream, a score system (15–60, with 60 as the most unstable) based on the channel bottom component of the Pfankuch index (Pfankuch 1975) was applied to each site. This index provides an assessment of channel stability by scoring several physical variables (weighted according to their perceived importance) and summing all values to generate an overall stability rating (Collier 1992). Stream slope at each site was measured using a transparent plastic tube carrying flowing water from the upstream to the downstream end of the reach. The slope was calculated as the difference between the water level inside the tube when raised until flow stopped and that of the surface of the stream water at the downstream end divided by the distance between the upstream and downstream end of the tube (c. 25 m). All measurements were performed during the morning before glacier meltdown, during the last months of the rainy season when lower discharge fluctuations are expected (compared to the dry season). Additionally, from March 2010, 3 months of daily temperature and pressure measurements were obtained, by installing water pressure loggers (Hobo water pressure loggers, Onset Computer Corp., USA) at each site. One more logger was fixed on a rock at 4100 m a.s.l. to measure atmospheric pressure. All loggers

were set to take measurements every 30 minutes. Water level and height between the stream bottom and the Hobo sensor were measured twice, when the loggers were installed and when they were removed. To calculate stream depth, water pressure values were transformed into water level values by subtracting the atmospheric variations from the water pressure data (Cauvy-Fraunié et al. 2014).

4.3. Glaciality index

During the last decade several methods to describe GI on streams have been developed (Brown et al. 2010). Each method has been constructed in accordance to the design of the study, working with either continuous, semi continuous or discrete data (Brown et al. 2003; Ilg & Castella 2006; Brown et al. 2009; Cauvy-Fraunié et al. 2013; Jacobsen & Dangles 2012; Jacobsen et al. 2012). Brown et al. (2003, 2009, 2010) designed a discrete classification of alpine streams, based on proportions of source water contribution inputs, to assess spatio-temporal variability. Cauvy-Fraunié et al. (2013a) defined the Wavelet Glacier Signal (WGS), which delivers continuous data based on wavelet analyses on water depth time series. Jacobsen & Dangles (2012) obtained a standardized, continuous index of glacial influence by combining glacier size with distance from the glacier terminus. Jacobsen et al. (2012) used the percentage of glacier cover in the catchment as an index, to compare data from three different continents. To assess the direct effect of glacier influence over trophic function, continuous data was essential. In our case, stream junctions lessen the glacier influence of pure glacier fed streams, regardless of distance, glacier size or catchment proportion. A method that integrated the distinctive environmental variables of tropical glacier fed streams was required. This requirements were accomplished by Ilg & Castella's (2006) continuous index for European alpine streams, based on water temperature, conductivity, suspended solids and Pfankuch index. However tropical Andean streams and glaciers are somewhat different (Jacobsen 2008;

Favier et al. 2008); i.e. in Alpine streams annual temperature variation is high and daily variation is low; while in Andean streams annual temperature variation is low and daily variation is high (Jacobsen et al. 2010). Thus, for this study we created a new Glaciality Index, slightly modified from the one proposed by Ilg & Castella (2006). Our index was based on stream conductivity, turbidity, Pfankuch index, and coefficient of variance (CV) of temperature and discharge. GI for each site was determined by obtaining the 1st component values of a non-centered principal component analysis (NPCA) (Ilg & Castella 2006) on these five variables (log transformed). For each abiotic variable we obtained and compared coefficient of variance along our Glaciality Index.

4.4. Primary feeding sources (PFS)

We measured the amount of two PFSs: 1) coarse particulate organic matter (CPOM), comprising particles larger than 1 mm, mostly allochthonous organic matter (organic matter from outside the stream), and 2) periphyton growing on the riverbed, on submerged surfaces exposed to light as an autochthonous resource. Five Surber net samples (500 cm^2 and mesh size 200 µm) were obtained to measure the amount of CPOM. After collecting the macroinvertebrates, we filtered the benthic detritus present in each Surber sample, through a 200-µm sieve. Then, this material was dried at 80 C° for 24 h, weighed and the mass loss upon combustion at 550 C° was taken as the amount of ash-free dry mass of organic material >200 µm in the sample.

Chlorophyll a (ChloA) concentration was calculated as a measure of benthic algal biomass at each site. For this, we collected 15 pebbles at random at each site (avoiding those with filamentous algae). Pebbles were placed in five containers (three in each), covered with 96% ethanol, and left for 1–3 days in the dark until further processing in the laboratory. Later the containers were given a 10-min ultrasonic bath to increase extraction efficiency. After

settlement for a few hours, a sample was transferred to a spectrophotometer and absorption was measured at 665 and 750 nm. Concentration of total chlorophyll a (including phaeopigments) was calculated according to Københavns Universitet (1989). Stone surface area was estimated using the formula A = (LW) + (LH) + (WH) proposed by Graham et al. (1988) where L is length, W is width and H is height of the stones. Exponential regressions for the Glaciality Index Gradient (GIG) were generated for both PFS. To identify the abiotic variables that exert greater effects on PFS distribution along the GIG, linear regression analysis was performed to obtain Variable Inflation Factor (VIF) values. Which provides an index that measures how much the variance of an estimated regression coefficient is increased because of collinearity (Kutner et al. 2004).

4.5. Populations and functional feeding groups

Quantitative data on macroinvertebrate assemblages at each stream reach was obtained from the aforementioned Surber samples. In order to standardize records, sampling was performed on areas with obvious flow. Samples were preserved in 75% ethanol. Macroinvertebrates within each sample were identified to the highest taxonomic resolution possible using local and regional taxonomic reference literature (Roldán 1996; Domínguez & Fernández 2009) and counted using a stereoscope OLYMPUS SZ-6145. Because of the currently limited taxonomic knowledge of neotropical taxa, identification of larvae to species level is practically impossible (Tomanova et al. 2006).

FFG reflect the functional role of organisms in their ecosystems and how their presence alters rates of ecosystem function (Ramirez-Guitierrez 2014). Determination of macroinvertebrate FFG was essential to understand their effect on organic matter degradation. Gut Content Analysis (GCA) certainly provides information on resources eaten and thus it would serve as a way to infer the FFG. Nonetheless, care must be taken to not assign groups

solely on what it is found in guts (Ramirez-Guitierrez 2014). FFG classification is the result of two key aspects used by macroinvertebrates when consuming resources: morphological characteristics (e.g., mouth part specialization) and behavioral mechanisms (e.g., way of feeding) (Ramirez-Gutierrez 2014). However, the assignment of a taxon to a single FFG category can lead to inaccurate characterization of biological/ecological taxa profiles (Chevenet et al. 1994). In our case, GCA targeted taxa with evidence of high feeding plasticity (Dangles 2002), i.e. lacking specialized mouth parts (less specialized: more generalist). Generalist strategy is known to be best adapted during unpredictable changes in primary resources dynamics (Albariño & Díaz Villanueva 2006). Because GI environmental severity affects primary resources dynamics (Zah & Uehlinger 2001; Tockner et al. 2002; Gessner et al. 1999; Robinson & Gessner 2000; Benfield 1997), our study required combinig FFGs and GCA to assess different levels of generalism. To avoid work overexertion and feeding guild effect misrepresentation, only representative genera were chosen for GCA. Each of these genera had to be abundant at any level of GI, and to comprise high feeding plasticity (Dangles, 2002). This information was verified from the literature and compared between authors when possible (Cummins & Klug 1979; Armitage et al. 1995; Convey & Block 1996; Merritt & Cummins 1996; Roldán 1996; Henriques-Oliveira et al. 2003; Motta & Uieda 2003; Bouchard 2004; Tomanova et al. 2006; Silva et al. 2008; Domínguez & Fernández 2009; Clitherow et al. 2013; Rico & Quesada 2013; Rivera et al. 2013). Twelve taxa matched these conditions: *i*) *Hyalella sp.* (Hyalellidae) *ii*) *Claudioperla sp.* (Gripopterygidae) *iii*) *Andesiops sp.*(Baetidae), *iv*) *Anomalocosmoescus sp.* (Limnephilidae), *v*) *Mortoniella sp.* (Glossosomatidae), *vi*) *Orchrotrichia sp.*, *vii*) *Neotrichia sp.* (Hydroptilidae) *viii*) *Prionocyphon sp.* (Scirtidae) *ix*) *Neoelmis sp.* larvae, *x*) *Neoelmis sp.* adult (Elmidae), *xi*) *Blepharicera sp.*(Blephariceridae) and *xii*) *Molophilus sp.*(Limoniidae).

Individuals where obtained from Surber samples from ten sites covering the whole GIG (G1, G2, GD1, GSDS1, GSD1, GDSS1, S1, D1, D2, S3 and S4) (Fig. 1). For each of the ten taxa, GCA was performed on 10 individuals (one individual per site). For those taxa that were not found at all 10 sites, randomly picked individuals from other sites were included to complete 10 individuals. The assignment of each taxon to a functional feeding guild depends mainly on the size, type and proportion of food in the intestinal content (Cummins, 1973). Five categories of feeding resources where recognized: i) filamentous algae, ii) diatoms, iii) coarse detritus, iv) fine detritus, and v) animal tissue (similar to Dangles, 2002). Categories were assessed in a semi quantitative manner, by estimating de proportion of each resource type within each foregut. Feeding habits of taxa that were not chosen for GCA, were obtained from local and regional literature (Cummins & Klug 1979; Armitage et al. 1995; Convey & Block 1996; Merritt & Cummins 1996; Roldán 1996; Henriques-Oliveira et al. 2003; Motta & Uieda 2003; Bouchard 2004; Tomanova et al. 2006; Silva et al. 2008; Domínguez & Fernández 2009; Clitherow et al. 2013; Rico & Quesada 2013; Rivera et al. 2013). FFG determination was achieved by analyzing GCA and referential data with a Paired Group Cluster Analysis (PGCA) with Euclidean similarity measures, using PAleontological STatistics (PAST) software (Hammer et al. 2001). Benthic samples' taxon abundance was assigned into FFG classification in order to analyze distribution of feeding guild's relevant biotic variables, such as richness, abundance, Buzas and Gibson's evenness, and Fisher's Alfa diversity indices along the gradient of glacial influence. Richness and abundance are expected to vary along the stress gradient and so should their effect over food sources and organic matter fragmentation. Evenness explains numeric population differences between sites along the gradient. Fisher's Alfa accounts for high abundance variation between sites, fitting better to a log series distribution. The relationship between FFGs, PFSs and GIG, was analyzed with

a canonical correspondence analysis (CCA). Additionally, a SIMilitude PERcentage (SIMPER) analysis was used to identify the FFGs that contributed the most to the CCA's dissimilarities between sites. For this, sites where classified in two groups, whether its CCA's 1st axis value resulted positive or negative. All analysis were performed using PAleontological STatistics (PAST) software (Hammer et al. 2001).

4.6. Organic matter decomposition

Decomposition of common páramo grass *Calamagrostis intermedia*, was measured as mass loss using 5 g of leaf blades placed in litterbags (15 x 10 cm) of two different mesh sizes (0.3 and 5 mm). The fine-mesh bags excluded macroinvertebrates, but coarse-mesh bags did not. Abscised leaf blades were representative of those that enter streams (Dangles et al. 2011). Three replicate bags of each type were secured both to the substrate and to the bank with plastic-coated wires. Installing 51 bags of each type, for a total of 102 bags at all 17 sites. The exposure started at the beginning of March 2010 and lasted for 12 weeks, a time sufficient to show significant decomposition, as several streams showed 60% leaf mass loss at the end of the exposure (Bärlocher 2005). After retrieval the grass material was rinsed to remove fine particulate matter and invertebrates (Dangles et al. 2011). The remaining plant material was dried (48 h at 50°C), ashed (4 h at 550°C), and used to calculate ash-free dry mass (AFDM). Invertebrates were counted and identified to morphospecies using Dominguez and Fernandez (2009). Ash-free dry mass (AFDM) was used to estimate organic matter daily decomposition (DDC) rate (k), which was calculated using the following equation: $k=(M_0-M_t)/t$, where M_0 is the initial mass and M_t the remaining mass at time t (in days). To account the effect of temperature on Coarse Organic Matter Decomposition (COMD) (Ferreira et al. 2006), we calculated decomposition rate in degree days (DGD). For this we replaced time (t) with the sum of mean daily temperatures accumulated until retrieval day. Validity of experimental data

was tested by a one way ANOVA between bag types using Statistical Package for the Social Sciences (SPSS) software (Pardo & Ruiz 2002).

Difference between treatments was obtained by subtracting decomposition rate coefficients in fine mesh bags (k_{FM}) from those in coarse mesh bags (k_{CM}). We assumed that this difference (k_{CM} -k_{FM}) represented the effect of biotic activity, and was also considered in further analysis. We compared the two types of decomposition rates (DDC and DGD) against the GIG, expecting rates between treatments to be more similar at sites baring low temperature variation. To identify the most relevant driving factors of COMD along the GIG, we used Generalized Additive Models (GAMs) using the R package *MGCV*. Because temperature variation is a representative feature of tropical glacier fed streams (Jacobsen et al. 2010) and its variation proved to be relevant for our GI (Appendix 3) only DGD rates were taken into account for GAM. In the case of k_{FM}, only abiotic environmental variables were considered as independent variables in the GAM, because fine mesh treatments excluded macroinvertebrate activity. Ten abiotic environmental and non-redundant variables relevant to COMD were chosen for the models. For example, conductivity was excluded due to its low and unclear effect over COMD (Neher et al. 2003) and because it is correlated with other GI characteristic variables like stability and O_2 (saturation and concentration) (Appendix 3). pH was also excluded because, although it affects COMD (Dangles et al. 2004), it is not a representative variable of GI (low CV along the GIG). Finally, benthic FFG ecological variables were tested against both COMD rates; k_{CM} and biotic activity (k_{CM}-k_{FM}).

5. RESULTS

5.1. Glaciality index, environmental variables and food sources

Glaciality Index values for the 17 sites were obtained from the NPCA. The first two axes accounted for 82% and 15% of the total variability, respectively (Table 1). Of the five chosen variables, turbidity was the one that most contributed (first axis loading value of 0.92) for defining this gradient. The following most contributing variables were conductivity, temperature CV and Pfankuch index. Temperature and depth CV had low contribution values. The first component loading values provided a very well distributed gradient in GI, from 0.328 and 0.297 at the two purely glacier-fed sites (G1 and G2 respectively) to 0.129 and 0.160 at the two spring streams (S4 and S3, respectively) (Fig. 2 and Appendix 1).

Depth variation over time was the most fluctuating variable along the GI gradient, with CV ranging from 0.00128 at G1 to 0.0074 at S1 (Appendix 2 and 3). Discharge was the second most fluctuating variable, ranging from 149 l/s at site G1, to 1 l/s at D1. Turbidity also presented high variability among sites, ranging from 284 NTU (G2) to 1.32 NTU (S4). Conductivity (from P2 = 214.4 μS*cm-1 to G2 = 12.2 μS*cm-1), temperature CV (from G1 = 0.4178 to S4 = 0.0002) and current velocity exposed intermediate variation along the gradient. Average current velocity ranged from 0.69 m/s (GSDSGDSS1) to 0.06 m/s (D1). Maximum and minimum velocities were highest at site GSDS1 (1.25 and 0.17 m/s), while site D1 had the lowest values along the gradient (0.15 and 0.01 m/s). Chemical variables such as pH (from S3 = 8.08 to S4 = 6.51), oxygen concentration and saturation (from S1 = 10.52 mg/l, 155% to G1 = 6.51 mg/l, 97%) presented little variation along the GI gradient. Channel stability, according to Pfankuch index (from P2 = 42 to G1 = 22) and depth (from S4 = 38 cm to S3 = 12 cm) didn't present much variation as well. The effect of GI over each

physicochemical variable and correlations between these variables are displayed in Appendix 4 and 5 respectively.

Average CPOM quantity was 10.5 g/m^2 and average ChloA concentration was 0.04 g/m^2 (Table 2). Although CPOM and GI did not present a significant relationship (R^2 = 0.019, p = 0.607) CPOM variation was higher at high GI (Fig. 3a). There was a weak (non-significant) negative relationship between ChloA and GI (R^2 = 0.161, p = 0.112), and slightly higher variation could be perceived at lower GI (Fig. 3b). According to VIF values of the linear regression analyses, current velocity (CPOM=222.7; ChloA=147.1) and oxygen availability (CPOM=222.7; ChloA=147.1) were the two environmental variables most related with food resources distribution (Appendix 6).

5.2. Diet and functional feeding group affiliation

Benthic samples collected a total of 123 040 individuals belonging to 27 taxa (Appendix 7 and 8). Note that in order to enhance statistical reliability of quantitative multivariate analysis we excluded rare species (taxa with less than 60 individuals in total) from results and analyses (Greenacre, 1984; Stevenson & Cook, 1980; Manté et al. 1995; Tomanova et al. 2006). Coarse and fine detritus were the most frequently ingested items for most of the twelve examined taxa. Periphyton and diatoms were less ingested and animal parts were rarely found in GCA. As an additional observation, mineral material in different proportions was observed in GCA of most individuals. Diet composition from GCA and literature assessment were obtained for all 27 taxa (Table 3) and clustered by the PGCA into nine FFGs (Fig. 4). Groups include scrapers that consume resources that grow attached to the substrate by removing them with their mouth parts; shredders that cut or chew pieces of living or dead plant material, including all plant parts like leaves and wood; collectors-gatherers (gatherers) that use modified mouth parts to sieve or collect small particles (<1mm) accumulated on the stream

bottom; collectors-filterers (filterers) that have special adaptations to remove particles directly from the water column; and predators that consume other organisms using different strategies to capture them (Ramírez & Gutiérrez-Fonseca 2014). However, in tropical ecosystems, some organisms do not fit in a single FFG or their behavior and function may vary over space and time (Ramirez-Gutierrez 2014). Taxa with less specialized mouthparts (i.e. in the case of insects, primitive mandibulate mouthparts for biting chewing and grinding) will be able to ingest a wider range of food items (Cummins 1973; Chapman 1998; Albariño & Díaz Villanueva 2006). Based on this statements, our shredders/scrappers are organisms that ingest both pieces of living or dead plant material and resources that grow over substrates (Ramirez-Gutierrez 2014). Benthic taxon abundance obtained from Surber samples were grouped according to these nine FFGs (Appendix 9). PGCA identified five specialist feeding groups (predators, scrapers, shredders, gatherers, and filters) and four groups with more generalist feeding habits (predators/scrapers, predators/gatherers, shredders/scrapers, and shredders/gatherers). Predators were the feeding group with most taxa (5 taxa, 18.5%); as some of them are well adapted to GI, while others inhabit only spring and superficial drainage. Followed by shredders and scrapers with four taxa each (14.8%), and collectors (gatherers and filters) with just three taxa each (11.1%). All generalist groups contained two taxa (7.4%).

5.3. Macroinvertebrate feeding assemblage metrics

Gatherers was the most abundant feeding guild (29.2%, 2069 ind/m^2), as highly abundant Chironomidae (Diptera) (26%, 1839 ind/m^2) were clustered within this group. *Hyalella sp.* (Hyalellidae), the most abundant taxon (26.1% of all collected individuals, 1850 ind/m^2) was clustered within the shredders/scrapers guild, the second most abundant FFG (26.4%, 1868 ind/m^2). Scrapers were also well represented (25.3%, 1778 ind/m^2) due to the high relative

abundance of *Andesiops sp.* (Baetidae) (22.5%, 1592 ind/m^2). Finally, *Anomalocosmoecus sp.* (Limnephilidae) (5.2%, 376 ind/m^2) was the least abundant representative taxa, and was included in the shredders guild (7.5%, 525 ind/m^2), which was the fourth most abundant feeding guild along the GI gradient.

Benthic ecological metrics from feeding guilds were obtained (Table 4) and compared against the GI (Fig. 5). The taxon-richest site was GSDS1 with 26 taxa (Appendix 7) and nine feeding guilds (Table 4). In contrast, lowest taxon-richness was found at site G2 with only 13 taxa, even though those taxa represented eight feeding guilds. Several study sites included nine feeding guilds, some eight (D1, D2 and SP2), a few 7 (G2 and S1) and site S4 only six. Highest abundance was found at site P2 (17515 ind/m^2) and lowest at site G2 (1130 ind/m^2). According to Fisher's Alfa diversity index, feeding guilds at site G1 were the most diverse and those at site S4 the least. Site S4 had the highest FFG evenness and site P2 the lowest (Table 4). FFG abundance displayed most variation along the gradient, (Fig. 5a) and decreased towards higher GI (Fig. 5b). FFG evenness was the second most variable (Fig. 5a) and displayed higher values at more stable sites like springs and superficial drainage, while lowest values were found at intermediate levels of GI. Sites with the highest GI (GF sites) shared slightly higher evenness values (Fig. 5c). Fisher's Alpha diversity was the second least variable (Fig. 5a) and increased towards GI (Fig. 5c). FFG richness presented the least variation (Fig. 5a) and displayed its peak at intermediate to high levels of GI (Fig. 5b). Nevertheless, none of these regressions were significant (Fig. 5b and c).

5.4. Distribution of functional feeding groups

As expected, GI followed the CCA first axis (Fig. 6a), with study site distribution following this gradient. Results on FFG distribution indicated that shredders, shredders/scrapers, scrapers and predators are associated with ChloA, in streams with low GI; while Gatherers are

more closely related to CPOM than to GI. Strict gatherers were distributed towards high values of GI. Most generalist feeding habits, such as predators/gatherers, shredders/gatherers and predators/scrapers were also associated with higher GI values. High GI sites were located towards higher values along the first axis, and lower values at less glacier influenced sites. This distribution allowed us to perform the aforementioned SIMPER analysis. SIMPER results (Fig. 6b) revealed shredders as major contributors (22%) to the CCA's dissimilarities between sites, followed by predators/scrapers (17.3%) and shredders/scrapers (12.1%). On the contrary, Gatherers(4.9%), predators (6.8%) and gatherers (8.4%) were the least important in terms of dissimilarity between sites; as they presented wider distributions along the GI gradient.

5.5. Organic matter decomposition

Daily decomposition rates (DDC) were generally higher in coarse than in fine mesh bags, and this difference was significant (DDC P = 0.002; DGD P = 0.003; one-way Anova) (Fig. 7a and b). The highest DDC for coarse mesh bags (k_{CM}) were found at site GSD1 (DDC k = 0.0289 day^{-1}), while the lowest value was at site GDS1 (DDC k = 0.0093 day^{-1}) (Table 5). For fine mesh bags (k_{FM}) the highest decomposition rate was also found at site 2J-2 (DDC k = 0.0242 day^{-1}) while lowest value was at site GS1 (DDC k = 0.0047 day^{-1}). When accounting for temperature variation (DGD), site S2 presented the highest rate (DGD k = 8.06e^{-5} day^{-1}) for k_{CM}, and S4 (DGD k = 9.90e^{-5} day^{-1}) for k_{FM}. The lowest k_{CM} value was at site GDS1 (DGD k = 2.39e^{-5} day^{-1}) and lowest k_{FM} value at GS1 (DGD k = 1.33e^{-5} day^{-1}). Relative differences between average decomposition rates in coarse and fine mesh bags followed the same pattern, either expressed as DDC (k_{FM} = 0.210, k_{CM} = 0.325, k_{CM}-k_{FM} = 0.054) or DGD (k_{FM} = 0.110, k_{CM} = 0.174, k_{CM}-k_{FM} = 0.0.022) (Fig. 7c and d). Although none of the regressions were significant, we found highest decomposition rates at medium values of GI

for both k_{CM} and k_{FM} treatments. This was true for both DDC and DGD. The presumed shredder activity (k_{CM}-k_{FM}) as DDC displayed a similar, but weak humped-shaped relationship with GI (Fig. 7c), while calculated as DGD there was no signs of relationship with the GI (Fig.7d).

Results (Table 6) indicate that seven abiotic environmental variables were related with k_{FM}. Average temperature was the most dominant factor for k_{FM} along the GI gradient. Oxygen concentration and discharge also had highly significant effects, and average current velocity had significant effects on k_{FM}. Temperature CV, turbidity and channel stability (Pfankuch index) were related with COMD. GAM plots displayed increasing k_{FM} rates with decreasing average temperatures and lower temperature CV (Fig. 8a, b). Decomposition rates also increased with increasing discharge, O_2 concentration and turbidity (Fig. 8c, e, g). Low channel stability seemed to favor decomposition processes, as well as intermediate to high current velocity (Fig. 8d and f). FFG ecological variables were not displayed as their plot patterns were the result of the overlaying effects of afore mentioned abiotic environmental variables**.**

6. DISCUSSION

6.1. Glaciality index, environmental variables and food sources

Previous studies in temperate regions have shown that maximum water temperature is one of the main environmental variables determining macroinvertebrate community structure in glacial streams during the summer melt season, and that it is most important in Alpine glaciality gradient determination (Milner et al. 2001; Ilg & Castella 2006). Ilg and Castella (2006) found temperature, conductivity and substrate stability to be important for classifying streams along a gradient of glacier influence. In contrast, our study of an Andean GI gradient revealed turbidity as the most contributive variable for our glaciality index, followed by conductivity and temperature variation. This difference could be due to the fact that our slightly modified glaciality index was not tested only against glacier-fed (GF) streams, but against spring-fed (SP) and spring/superficial drainage-fed (SD) streams as well. For that reason, most contrasting features of glacier-fed streams, such as high concentrations of suspended solids (e.i. high turbidity), low conductivity and temperature variation (Milner & Petts 1994; Malard et al. 2000; Füreder et al. 2001; Jacobsen et al. 2010) contributed the most to our GI. In contrast with previous studies, we measured turbidity instead of suspended sediments (Ilg & Castella 2006), and did not take into account the variation in conductivity. Also, conductivity and temperature were measured during 3 h in alpine streams, while in our study, temperature CV was obtained from 3 months of logged data.

Benthic algae have been found to be the dominant energy source in temperate glacier-fed streams (Lavandier & Décamps 1984; McKnight & Tate 1997; Uehlinger & Zah 2003). Periphyton distribution is driven by variables which are also related with GI, like water temperature, bed load transport dynamics and concentration of suspended solids (Cattaneo et al. 1997; Horner et al. 2006; Kuhn et al. 2011). High daily temperature variation, together

with sudden increases in current velocity and suspended solids could raise periphyton loss rates and could explain lower periphyton quantities with higher GI found in this study. In fact, the study by Horner et al. (2006) found that loss rates of lotic periphytic algae increased with elevated, turbid storm discharges or high-flow events (Horner et al. 2006), which are precisely some of the environmental conditions that characterize tropical glacier fed streams. Additionally, part of the variability in algal biomass (measured as chlorophyll concentration) is positively related to substratum size (Cattaneo et al. 1997). And substratum size is one of the stability parameters used to obtain Pfankuch index, as smaller rock sizes attribute less substratum stability (Pfankuch 1975). Kuhn et al. (2011) also found that chlorophyll *a* interacted with stability in tropical glacier fed streams.

Riparian vegetation, in the form of grass and scrub in highlands, are expected to provide allochthonous CPOM. Nevertheless, in the tropics allochthonous organic matter inputs do not occur as short seasonal pulses (Cuffney & Wallace 1989; Lemly & Hilderbrand 2000). In our study we found that CPOM is not directly affected by GI, which explains its stable average along the gradient (Fig. 3b). However, CPOM variability was higher at higher values of GI. This variability may be explained in two ways: 1) High-flow events, such as daily glacier melt in tropical systems are prevalent forms of natural disturbance (Lake 2000, Bunn & Arthington 2002) that reduce food resources by carrying away benthic detritus and scouring benthic algae (Peterson & Stevenson 1992, Biggs et al. 1999); 2) Retention of benthic detritus within streams is controlled by heterogeneity and quantity of retention structures (i.e. rocky outcrops and debris dams), which reflect the geomorphologic and hydrological characteristics of the stream (Vannote et al. 1980; Webster et al.1994, Mathooko et al. 2001). Detritus is retained for shorter periods in turbulent and more instable catchments than in more stable ones (Cariss & Dobson 1997). High flow events, low riverbed stability

(i.e. low heterogeneity) and high current velocity are common features of tropical glacier fed streams (Jacobsen et al. 2010; Kuhn et al. 2011). These features reduce organic matter retention and increase its fragmentation (Carris & Dobson 1997; Mathooko et al. 2001; Kuhn et al. 2011). This suggests that GI constrains CPOM distribution, which in turn, may affect feeding resource availability for some FFGs. It is important to note that particulate organic matter inputs from the riparian zone into stream channels are low or lacking at high latitude streams and alpine headwater catchments with sparse or no riparian vegetation (McKnight & Tate 1997; Zah & Uehlinger 2001).

6.2. Diet and functional feeding group affiliation

Most studies have estimated stoichiometric imbalances between consumers and resources by inferring the diet of the consumers from published functional classifications rather than by direct assessments of the diet (Lauridsen et al. 2014). Few studies about tropical macroinvertebrate FFGs have been obtained from practical analysis of species gut content (Tomanova et al. 2006; Motta & Uieda 2003). Because of this, we could only compare our results with the feeding habits of macroinvertebrates studied at the foothills of the Bolivian Andes (Tomanova et al. 2006). Using different methods Tomanova et al. (2006) accounted eight food resource categories, and grouped 49 taxa into three groups (predators, gatherers and generalists) and eight sub groups. According to the PGCA performed in this study there are nine feeding resource categories, that allowed us to classify 27 taxa into nine FFGs. Six taxa collected in both studies displayed high feeding plasticity: *i*) *Andesiops sp.*, *ii*) *Mortoniella sp.*, *iii*), *Ochrotrichia sp.*, *iv*), *v*) *Neotrichia sp.* and both stages of *vi*) *Neoelmis sp.*(larvae and adult). *Andesiops sp.* populations in the Bolivian Andes presented Gatherers feeding habits (mostly gatherers); while in our study they were grouped as scrapers (Fig. 4). Feeding habits may switch with life stage. Such is the case of *Neoelmis sp.*, which displayed feeding habit

plasticity between life stages in both studies. Bolivian larvae included scrapers/gatherers/shredders feeding habits (mostly scrapers/gatherers and slightly shredders) and adults gatherers (mostly gatherers). In contrast, Ecuadorian larvae were classified as shredders/scrapers and adults as shredders/gatherers. FFG assignation differences may be caused by disparity between methods, although deeper comparisons (between food categories) might suggest a change of diet mediated by environmental adaptation. Inferring whether or not the change is adaptive can enhance our knowledge about responses to climate change and should be tested in future studies (Ellegren & Sheldon 2008; Merilä & Hendry 2014).

6.3. Macroinvertebrate feeding assemblage metrics

Functional diversity of several life traits has been shown to increase significantly as glacier cover decreases in an arctic glacier fed stream (Brown & Milner 2012). Functional ecological variables assessed in our study (Fig. 5a) were obtained from just one functional trait (i.e. feeding assemblages). Feeding guild abundance was inversely related to GI (CV = 0.654) (Fig. 5b). On the contrary, FFG richness was less affected, as the few taxa present at higher GI represent several if not all feeding guilds; i.e. G1 presents almost half of all the taxa but they represent all feeding guilds (Table 4). Functional redundancy was also found in arctic glacier-fed streams, because new colonizers possess similar traits to taxa already present at higher glacier influence (Brown & Milner 2012). Functional redundancy may confer higher ecosystem resilience, because if a species disappears there are others that fulfill the same function (MacArthur 1955; May 1973; Tilman 1996; Tilman et al. 1996). This knowledge may be useful in the future management of biodiversity affected by glacial retreat caused by CC. Fisher's Alfa FFG diversity index was positively related to GI; fitting better to a log series distribution (Fisher et al. 1943). Thus, FFG diversity reached a better fit when taking into account feeding guild abundance variation caused by GI. Finally, FFG evenness was also

positively related to GI, as environmental harshness may regulate macroinvertebrate colonization more uniformly at high influenced sites (Milner et al. 2001). Corroborating with this suggestion, niche filtering processes in arctic systems have been found to predominate at extensive glacial cover, reflecting water temperature and dispersal constraints (Brown & Milner 2012). Downstream, in mainstream reaches communities shift towards co-occurrence of stochastic and deterministic assembly processes (Brown & Milner 2012).

6.4. Distribution of functional feeding groups

Resources vary along streams producing a continuous mosaic of communities adapted to such variation (Vannote et al. 1980). Primary production is the main source of organic matter in glacial streams above the treeline (Howard-Williams et al. 1986; Suren & Winterbourn 1991; Milner & Petts 1994; Pandey et al. 1995), and affects number of taxa, species composition, population dynamics and ecosystem functioning in interaction with stream stability (Winterbourn & Ryan 1994; Peterson et al. 1998; Kuhn et al. 2011). Efficiency and abundance of shredders may be dependent on stream type, native riparian composition and extent, retention capabilities and the allocthonous/autocthonous organic matter ratios (e.g., Rounick & Winterbourn 1983; Dangles 2002; Jonsson et al. 2002; Dangles et al. 2011).Dobson and Hildrew (1992) suggested that leaf litter may be a limiting resource (as are habitat and food) for shredding insects in lowland streams. Similar conditions may exist in glacial streams exhibiting physicochemical environmental stress (low conductivity, high temperature CV and turbidity); and lacking riparian inputs (Robinson et al. 1998). In accordance with previous results, our CCA (Fig. 6a) indicates that autochthonous and allochthonous sources (ChloA and CPOM) are affected by GI. The same was observed with the distribution of shredders, scrapers predators and shredders/scrapers, preferring more stable streams as they struggle to avoid imbalances between the supply and the demand of resources

(Lauridsen at al. 2014). The SIMPER analysis (Fig. 5b) pointed out shredders as the major contributor to CCA distribution. Shredders distribution towards streams with lower glacier influence is not only directly related to physicochemical harshness, but also indirectly to PFS availability; probably leading to different levels of intra specific competition (Richardson 1991). In our study, herbivore distribution seems to be affected due to the physicochemical features of GI, lower organic matter retention and increase its fragmentation. According with our findings, in severe environments, opportunistic generalist habits (predators/gatherers, shredders/gatherers and predators/scrapers) might prevail over specialization on a single food resource allowing them to inhabit a wider range of environments (Krebs et al. 2012; Townsend et al. 2008).

6.5. Organic matter decomposition

In several lotic systems, decomposition rates may depend on shredder richness more strongly than on abiotic forces (Jonsson et al. 2001; Cornwell et al. 2008; Encalada et al. 2010). In Alpine glacier influenced systems, highest decomposition rates are reached at lake outlets –which may be considered as intermediate glacier influence sites, –while the lowest rates are obtained at high influenced pro-glacier sites (Robinson et al. 1998). Our study yielded similar results with highest decomposition rates for coarse mesh packs (k_{CM}) at site 2J-2, which shows an intermediate GIG value (Table 5 and Fig. 7c). As expected, k_{CM} rates were higher than k_{FM} which is usually explained as the addition of the effect of macroinvertebrates (Robinson et al. 1998; Wright & Covich 2005). However, Andean decomposition rates are high and differences between treatments are narrow, especially for DGD (Fig. 7d). This may imply that environmental variables related with GI drive stronger effects over COMD than expected; this statement will be discussed later.

Corroborating with our results, differences in macroinvertebrate composition appear to play a role in the observed differences in breakdown rates among alpine glacier stream types. For example, the large alpine shredding trichopteran *Acrophylax zerberus*, present only at low alpine sites, enhances breakdown rates (Robinson et al. 1998). In Andean highland streams, decomposition rates were lower in streams with low values of both shredder taxon richness and abundance (Dangles et al. 2011). Like Dangles et al. (2011), we also collected *Anomalocosmoecus sp.* morphospecies and classified it as a shredder. The distribution of this morphospecies proved to be affected by the GI. Our study follows the same pattern mentioned before; COMD rates were higher at intermediate levels of GI (Fig. 7c and d; Robinson et al.1998), probably due to the combined effects of higher average temperature (Ferreira et al. 2006) and higher shredder richness.

Leaf breakdown rates and fungal respiration rates increased with water temperature, as high temperature favor decomposition by increasing microbial activity (McClaugherty et al. 1985; Cornejo et al.1994; Ferreira & Chauvet 2011; Eusufzai et al. 2013). In accordance to this, GAM results on abiotic environmental variables (Table 5) identified average temperature as the main driving factor for COMD (k_{FM}) along the GIG. However, as opposed to that found in other studies (with different designs and conditions), in our study, higher average temperature decreased COMD (Fig. 8a) (Ferreira et al. 2006; Chergui & Pattee, 1990). Perhaps average temperature effects remained overlaid by the effect of other GI variables, holding stronger effects over COMD. Higher turbulence (high discharge and current velocity), O_2 concentration mediated by turbulence, temperature variation and turbidity are features of GI (Milner et al. 2001; Jacobsen et al. 2010) and were to enhance COMD in other studies (Carris & Dobson 1997; Ferreira et al. 2006; Horner et al. 2006; Wantzen et al. 2008; Ferreira & Chauvet 2011; Dangles et al. 2011). According to our results, COMD rates were higher at

lower temperature CV (Fig. 8b), as higher rates were found at sites baring intermediate GI and intermediate to low temperature CV values (Appendix 1). Additionally, more stable sites baring lower temperature CV harbored more densities of shredders (shredders and shredders/scrapers) (Fig. 6a), which may also explain the high COMD rates at intermediate GI. This may also explain GAM plots for stability index and current velocity (Fig. 8d and f). Discharge, O_2 concentration and turbidity confirmed their abrasive effect over COMD (Horner et al. 2006; Dangles et al. 2011) along our GIG (Fig. 8c, e and g). Thus, abiotic environmental variables characteristic of glacier influenced streams strongly directed COMD ratios.

According to GAM, abundance and evenness were the functional variables that direct stronger effects over COMD along the GIG. Increasing GI decreases individual densities (Burgherr & Ward, 2001; Robinson et al. 2001; Jacobsen et al. 2010). The effects of temperature variation, discharge and turbidity, over individual abundance and physical abrasion of coarse organic matter, may explain the overlapping effects of the abiotic environment over the ecological variables. As mentioned before, k_{CM} rates are higher than the observed in k_{FM} (Fig. 7a and b), which is supposed to be due to macroinvertebrate effect on COMD (Robinson et al. 1998; Wright & Covich 2005). It is possible, however, that likewise all other fine-mesh coarse-mesh decomposition experiments, some of this effect was caused by the physical differences between bag types (Benfield 2006). Litter within coarse mesh bags was more exposed to physical defragmentation than within fine bags, due to the slight protection provided by the organza thread against discharge, turbulence and suspended solids. Therefore, the design of our decomposition experiment might had been affected by GI driven variables such as turbulence, turbidity, oxygen and temperature. This study corroborates with the idea that glacier-fed stream ecosystems are unique among lotic systems in supporting

predictable macroinvertebrate communities because of the overriding dominance of physical variables in determining community structure (Brittain & Milner, 2001).

In conclusion, our results indicate that COMD follows a weak humped-shaped relationship along a gradient of glacial influence in high-Andean glacier-fed streams, that the abiotic environment seems to be responsible for this, and that the shredder-effect is, at the most, weak. At high GI, shredders probably "struggle against the environment" in order to attain their principal food source. In contrast, gatherers seem to benefit from GI's abrasive forces on organic matter, and by relieving interspecific competition. Similar to alpine streams, our study indicates that organic matter dynamics in tropical andean glacier fed streams bare low autochthonous production, low allochthonous input and retention, and constantly processing organic matter by physical abrasion (Zah & Uehlinger 2001; Tockner et al. 2002; Gessner et al. 1999; Robinson & Gessner 2000; Benfield 1997).This produces shifts in macroinvertebrate FFG relative abundance, as niche filtering processes take place along the GI gradient, attempting to avoid supply-demand imbalances (Vannote et al. 1980; Ward 1992; Wallace et al. 1995; Angradi 1996; Brown & Milner 2012; Lauridsen at al. 2014). Finally, this study provides insights on how CC induced melting and subsequent disappearance of tropical glaciers may drive the functional distribution of species, affecting the ecological resilience of streams under glacial influence. For a better understanding of CC repercussions on ecological resilience, it is a priority to assess GI effects on additional life traits like territorial and reproductive behavior and dispersal ability. As future CC might imply changes in altitudinal distribution of species, and in downstream environmental conditions for glacier associated streams; due to its melting and eventual diminish.

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8. FIGURES

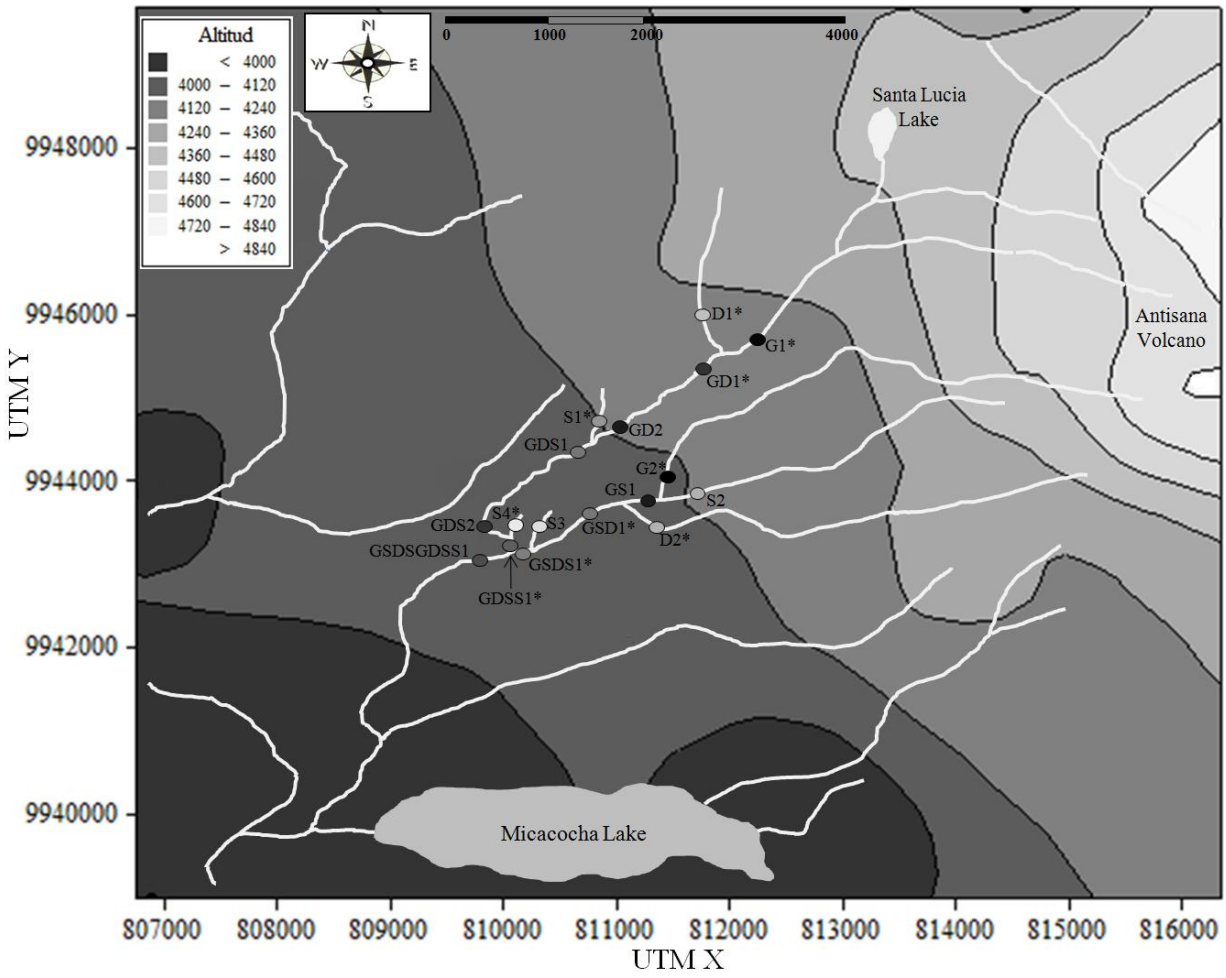


Figure 1. Location of study sites at the western foothills of the snowcapped Antisana volcano, named according to their source: glacier-fed (G), spring-fed (S), and superficial drainage (D). Site's gray scale represents the Glaciality Index Gradient (GIG). * Indicates the sites from where individuals were collected for Gut Content Analysis (GCA).

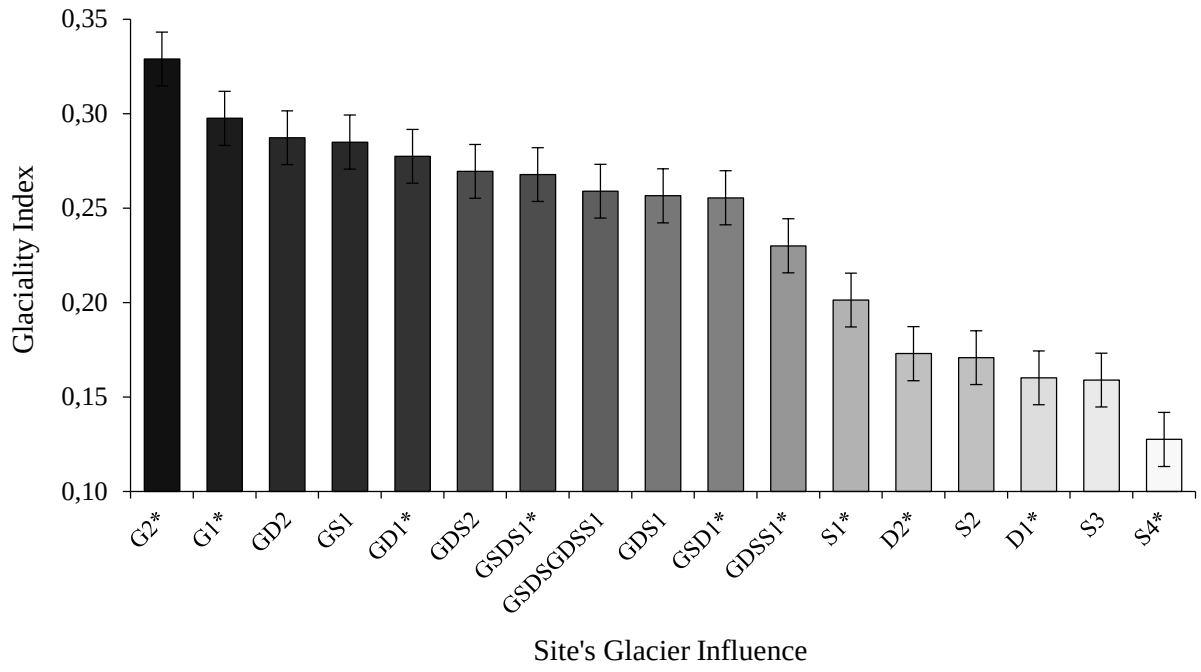


Figure 2. *Glaciality Index Gradient* (GIG) obtained from PCA's 1st component values (decimals) based on stream conductivity, turbidity, Pfankuch stability index, coefficient of variance (CV) of temperature and discharge data. Gray scale represents glacier influence intensity. * Indicates the sites from where individuals were collected for Gut Content Analysis (GCA).

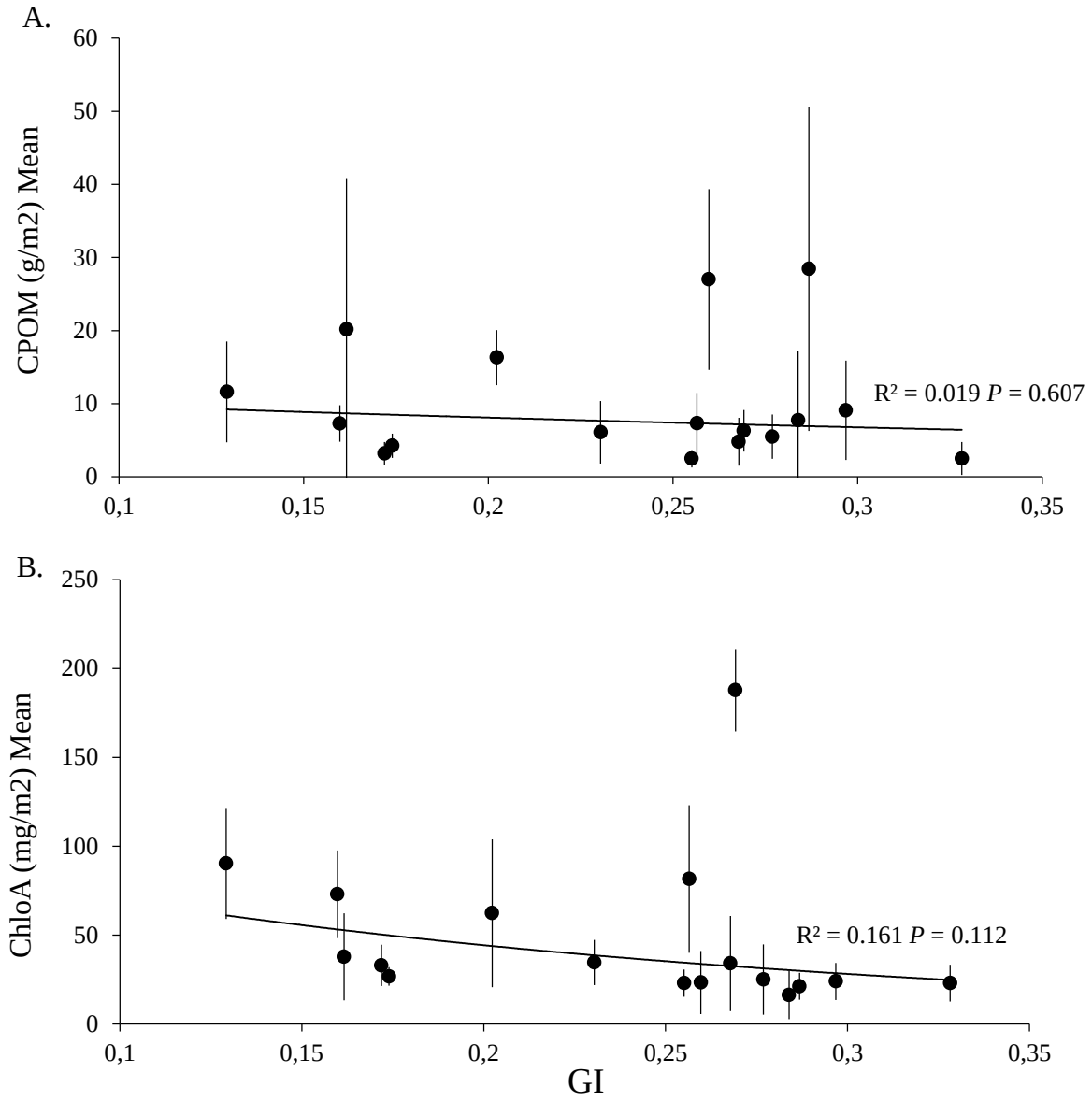


Figure 3. Polynomial regression for average quantity of primary food sources (PFSs) along the glaciality index gradient (GIG). a) coarse particulate organic matter (CPOM) and b) Chlorophyll A (ChloA). Vertical lines represent standard deviations.

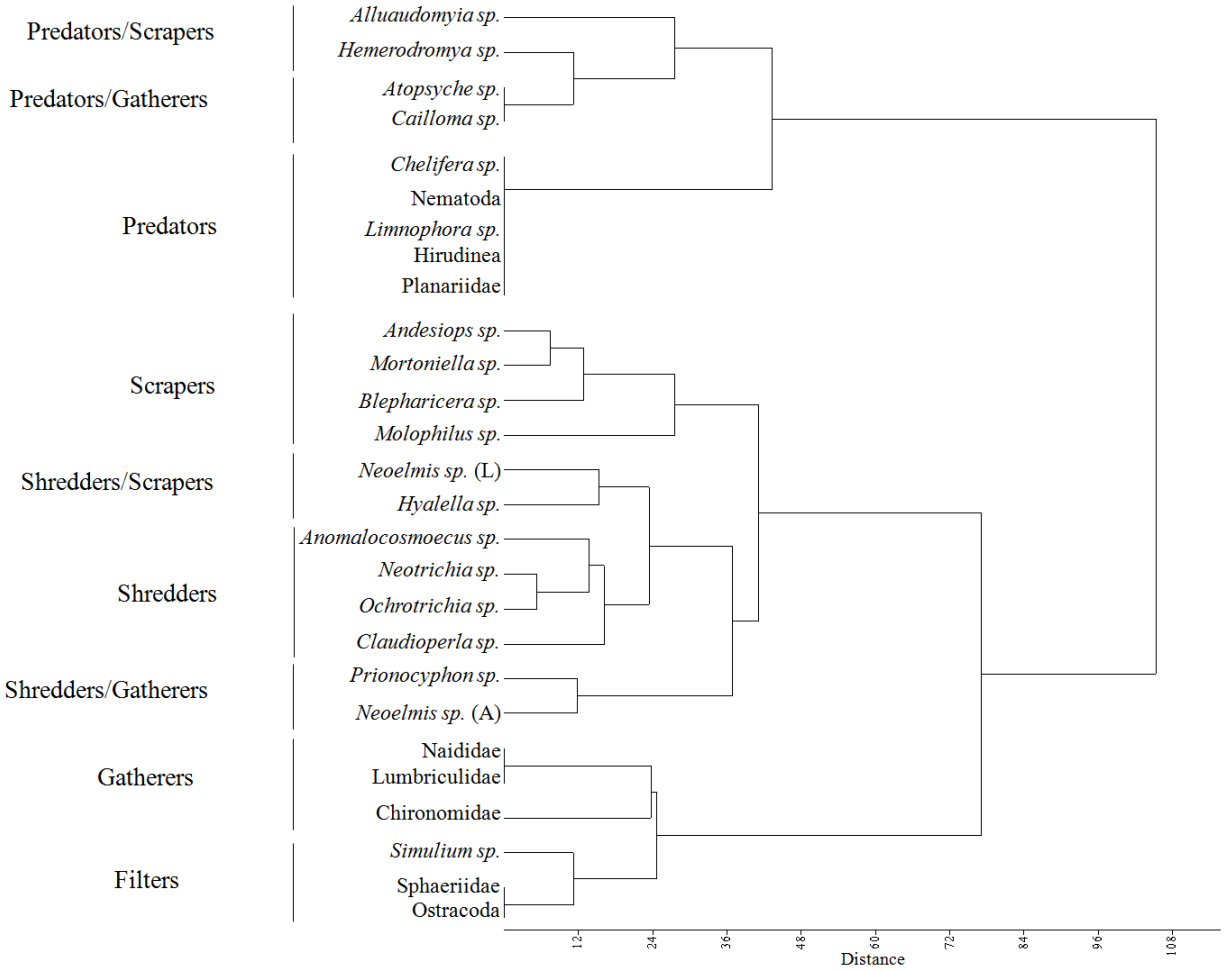


Figure 4. Functional feeding groups (FFGs) defined by a paired group cluster analysis (PGCA) of taxa. Using both GCA and referential diet data.

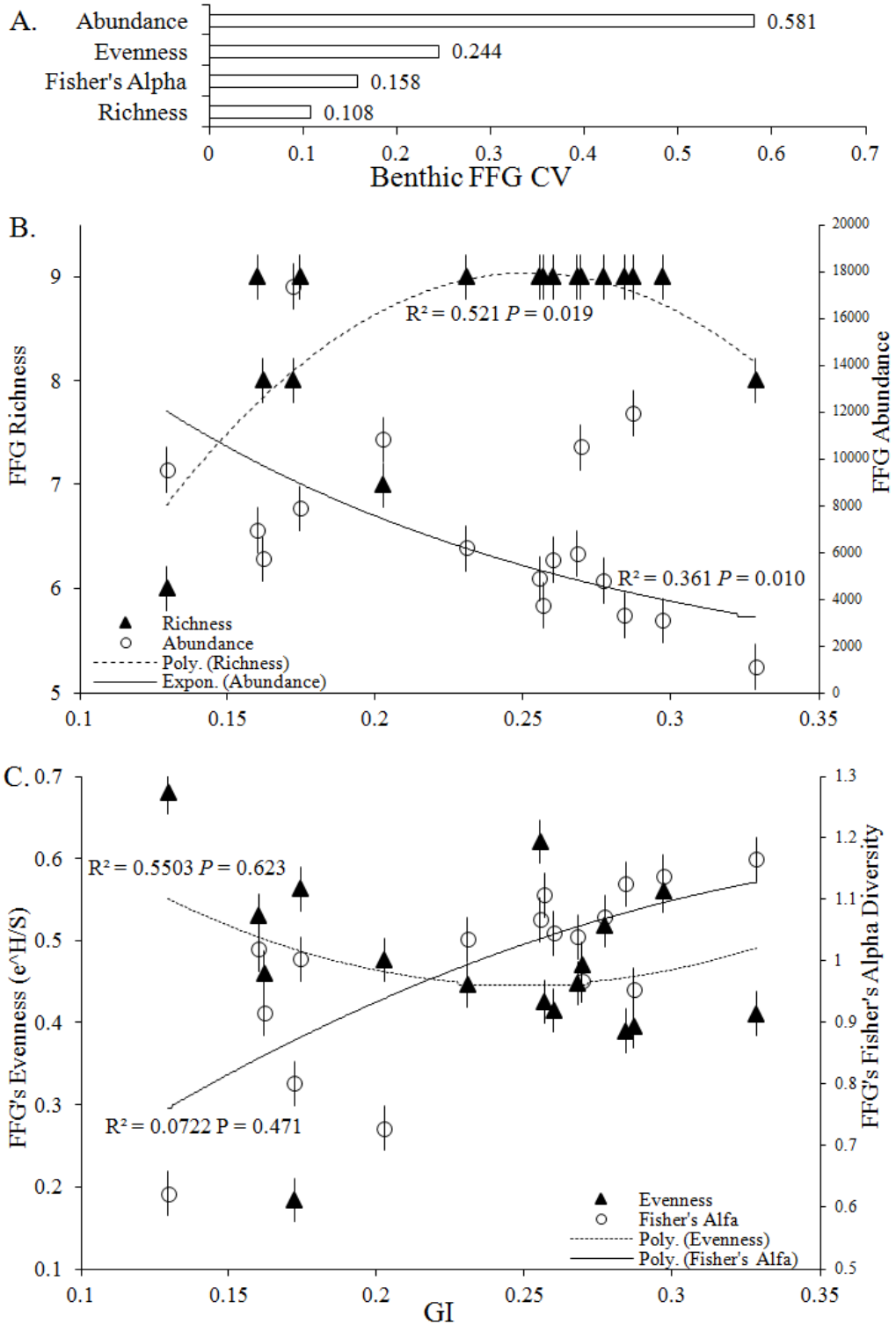


Figure 5. Relationships between feeding guild based fauna metrics and the glaciality index gradient (GIG); A) biological variables coefficient of variance along the GIG, B) FFG abundance and richness vs. GIG, c) Fisher's Alfa and evenness vs. GIG. Exponential and polynomial regressions were fitted to the data. Vertical lines represent standard errors.

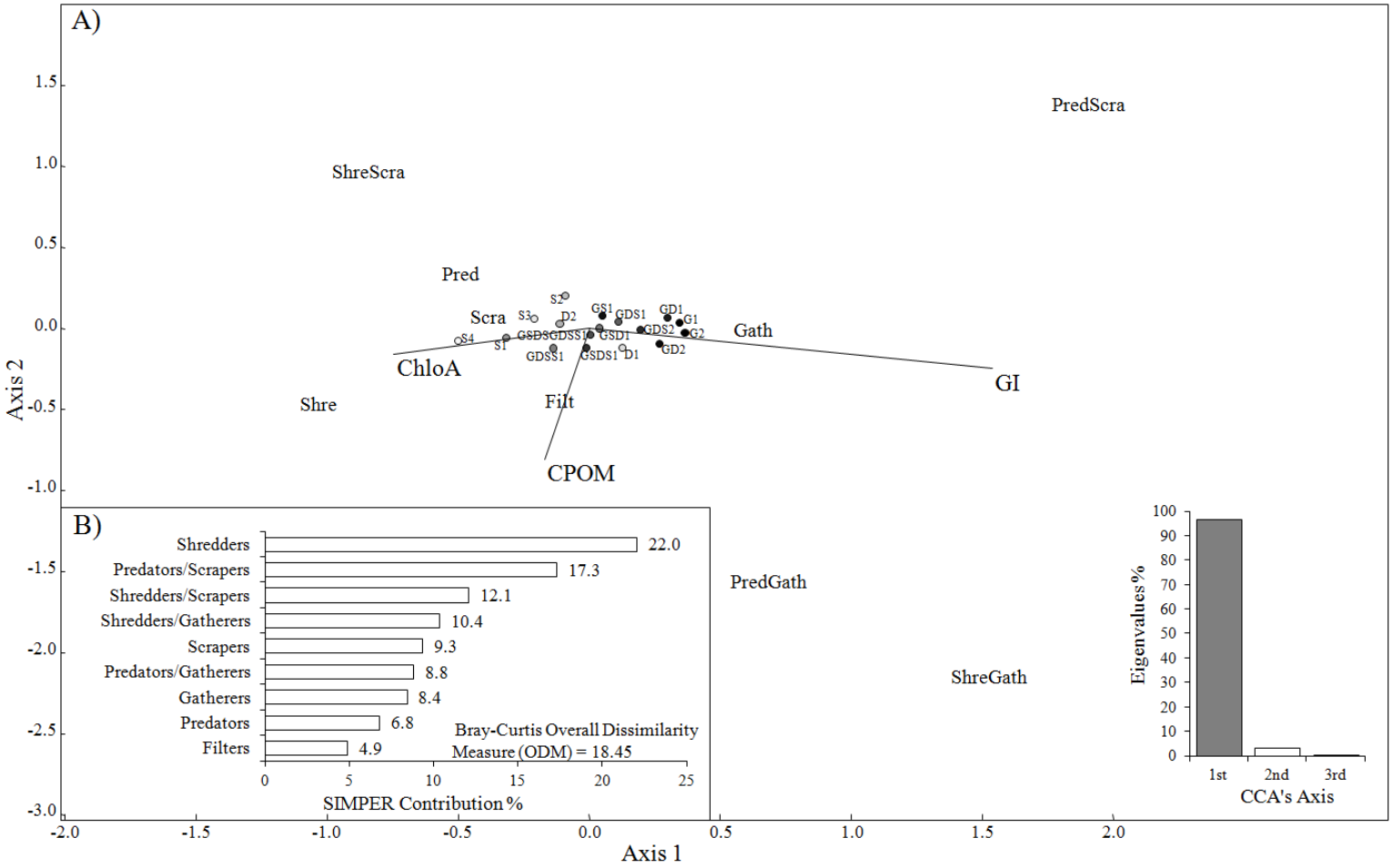


Figure 6. A) Canonical correspondence analysis (CCA) for primary food sources (PFSs) and glaciality index gradient (GIG). Environmental variables plotted as correlations with site scores (scaling type 1); including respective axis Eigenvalues. B) SIMilarity PERcentage analysis (SIMPER) results on functional feeding groups (FFGs) contribution to the CCA's dissimilarity.

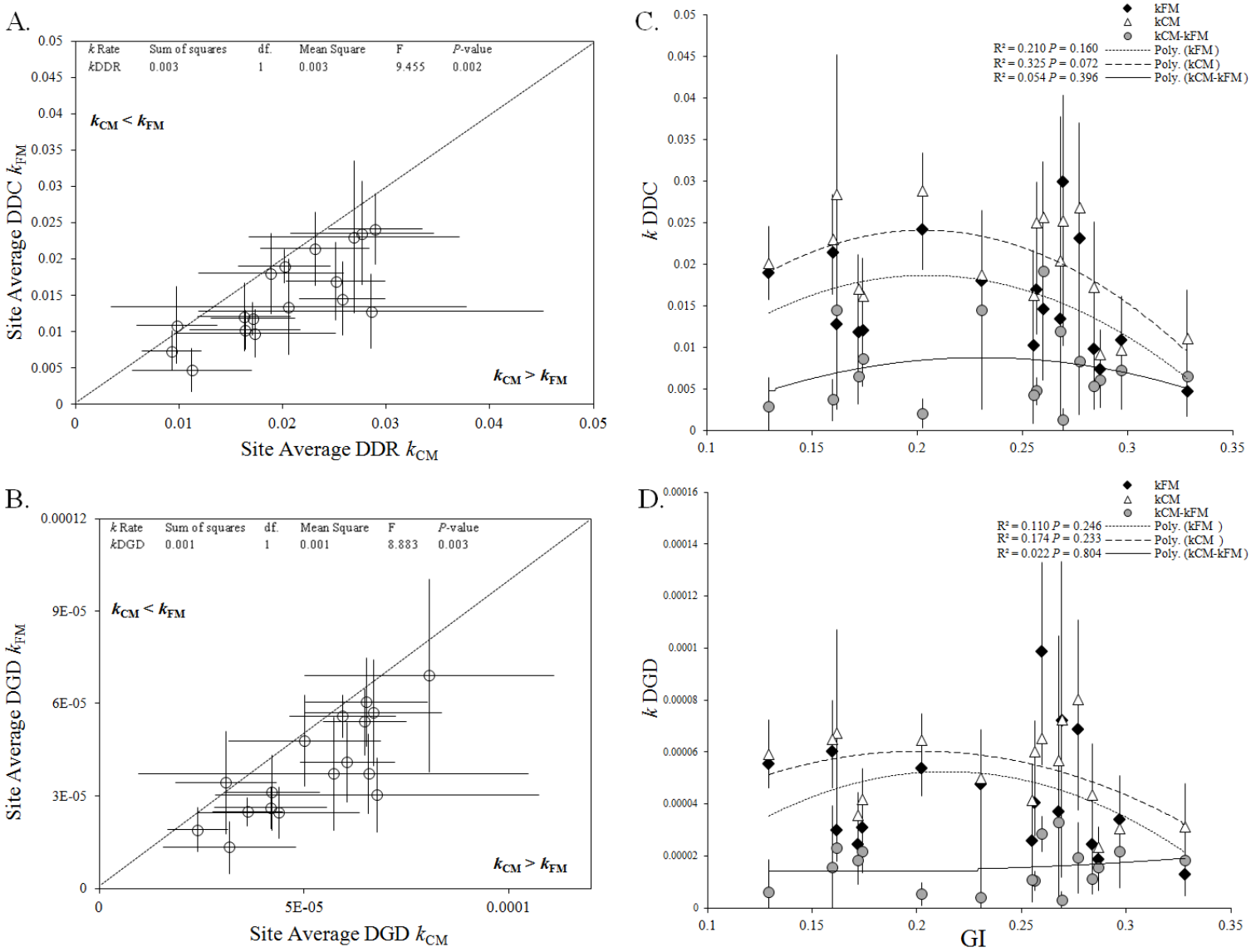


Figure 7. Average decomposition rate in A) days (DDC) and B) degree days (DGD,) of fine mesh (k_{FM}) and coarse mesh (k_{CM}) bags at the 17 study sites, including their respective one-way ANOVA results. Polynomial regression on C) DDC and D) DGD along the gradient, for fine mesh (k_{FM}, dotted lines), coarse mesh (k_{CM}, intermittent lines) and their difference (k_{CM}-k_{FM}, continuous lines).

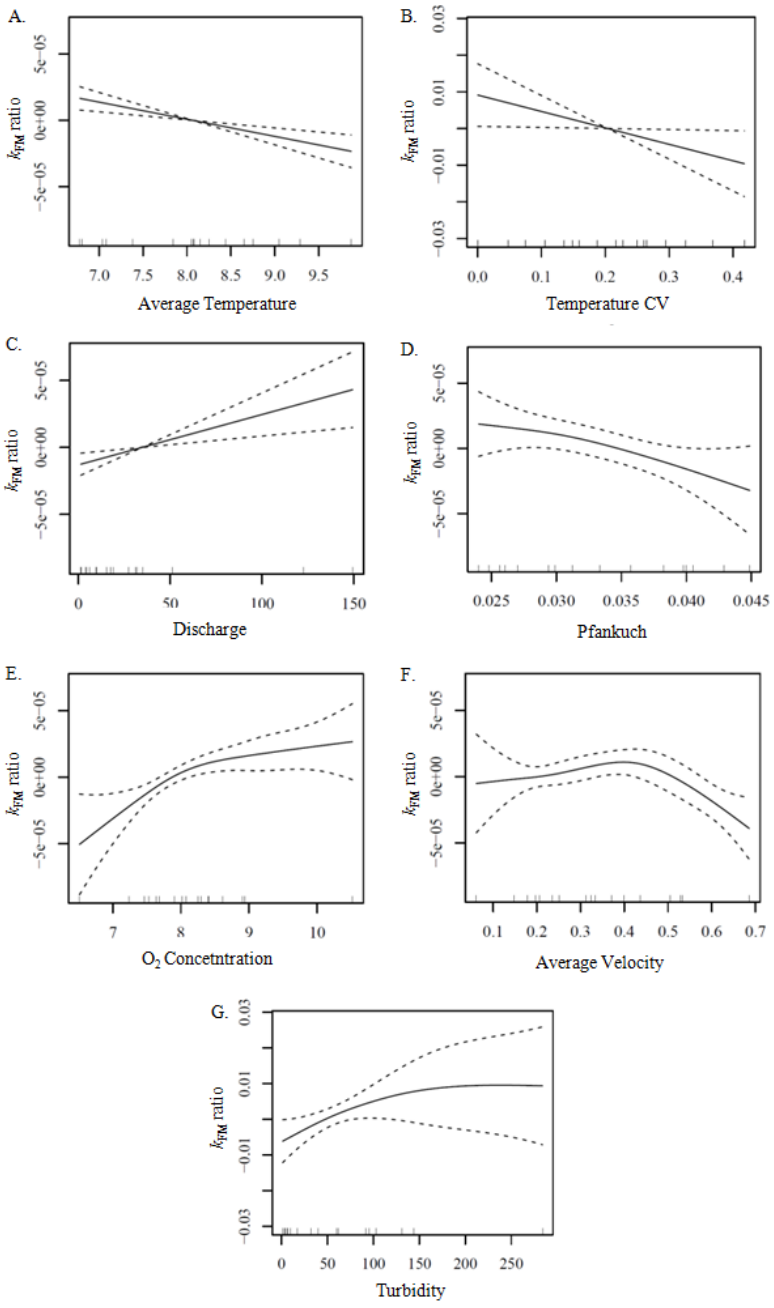


Figure 8. Generalized Additive Model (GAM) regression plots for those environmental variables that were found to be related and significantly related with organic matter decomposition (OMD) along the GIG. Horizontal axis show variable's value and vertical axis represent the variable's linear regression units for the designated OMD rate, and includes the effective degrees of freedom by the variable's name. Dotted lines represent the standard error of the estimates.

9. TABLES

Table 1. Loadings of the variables for the F1 and F2 axes of the non-centered PCA for the glaciality index.

Variables	1st Axis	2nd Axis
% Variance explained by each axis	0.82	0.15
Turbidity	0.92	0.37
Conductivity	-0.36	0.92
Temperature CV	0.11	-0.05
1/Pfankuch	0.09	-0.09
Temperature	-0.01	0.11
Depth CV	$3.50E^{-05}$	0.00

Table 2. Quantities of primary food resources.

Site	Average CPOM (g/m2)	CPOM CV	Average ChloA (mg/m2)	ChloA CV
G2	2.52	0.896	22.9	0.453
G1	9.09	0.748	23.9	0.437
GD2	28.46	0.779	21.2	0.356
GS1	7.75	1.228	16.2	0.834
GD1	5.50	0.551	24.9	0.793
GDS2	6.29	0.452	187.7	0.124
GSDS1	4.80	0.684	34.0	0.785
GSDSGDSS1	27.00	0.458	23.3	0.759
GDS1	7.31	0.569	81.5	0.509
GSD1	2.48	0.474	22.9	0.334
GDSS1	6.10	0.702	34.6	0.366
S1	16.31	0.232	62.3	0.667
D2	4.26	0.388	26.7	0.196
S2	3.19	0.490	32.9	0.353
D1	20.20	1.024	37.8	0.648
S3	7.30	0.341	72.9	0.338
S4	11.62	0.593	90.3	0.345

Table 3. Macroinvertebrate a) gut contents analysis (GCA) and b) referential diet composition (%).

	Periphyton	Diatoms	Coarse Detritus	Fine Detritus	Animal Parts
a) Gut Content Analysis					
Elmidae sp.Larvae	17	14	51	17	0
Elmidae sp. Adult	9	5.5	41	44	0
Prionocyphon sp.	16	4	32	47	0
Blepharicera sp.	14	42	10	32	0
Molophilus sp.	9	33	38	19	0
Andesiops sp.	19	33	14.5	32	0
Claudioperla sp.	24	15	38	19	3
Mortoniella sp.	19	33	20	27	0
Neotrichia sp.	32	14	45	8	0
Ochrotrichia sp.	28	15	48	8	0
Anomalocosmoecus sp.	37	8	38	10	6
Hyallela sp.	15	4	52	28	0
b) Referential Diet					
Sphaeriidae	0	0	0	100	0
Naididae	0	0	20	80	0
Lumbriculidae	0	0	20	80	0
Hirudinea	0	0	0	0	100
Alluaudomyia sp.	0	17	0	32	49
Chironomidae	0	16	2	78	1
Chelifera sp.	0	0	0	0	100
Hemerodromia sp.	0	9	0	23	66
Limnophora sp.	0	0	0	0	100
Simulium sp.	0	3	6	91	0
Atopsyche sp.	0	1.9	0	23	74
Cailloma sp.	0	1.9	0	23	74
Ostracoda	0	0	0	100	0
Planariidae	0	0	0	0	100
Nematoda	0	0	0	0	100

Table 4. Univariate fauna metrics calculated on proportions of functional feeding groups (FFG).

	Benthic			
Site	Richness	Abundance	Evenness (e^H/S)	Fisher's Alpha
G2	7	1130	0.413	0.99
G1	9	3043	0.496	1.14
GD2	9	12131	0.377	0.95
GS1	9	3288	0.402	1.13
GD1	9	4626	0.459	1.08
GDS2	9	10614	0.405	0.97
GSDS1	9	5830	0.414	1.04
GSDSGDSS1	9	5771	0.416	1.04
GDS1	9	3857	0.411	1.10
GSD1	9	4830	0.616	1.07
GDSS1	8	6205	0.485	0.91
S1	7	10956	0.475	0.73
D2	8	7737	0.629	0.88
S2	8	17515	0.192	0.80
D1	8	6276	0.515	0.90
S3	9	6973	0.532	1.02
S4	6	9544	0.681	0.62

Table 5. Decomposition rates (k = day^{-1}) of coarse bags (k_{CM}), fine bags (k_{FM}) and their difference (k_{CM-FM}), per day (DDC) and per degree days (DGD).

	DDC			DGD		
Site	k_{CM}	k_{FM}	k_{CM-FM}	k_{CM}	k_{FM}	k_{CM-FM}
G2	0.0202	0.0190	0.0030	5.94E-05	5.59E-05	6.34E-06
G1	0.0231	0.0214	0.0037	6.53E-05	6.05E-05	1.59E-05
GD2	0.0206	0.0134	0.0119	5.72E-05	3.73E-05	3.31E-05
GS1	0.0112	0.0047	0.0065	3.17E-05	1.33E-05	1.84E-05
GD1	0.0171	0.0118	0.0065	3.61E-05	2.49E-05	1.84E-05
GDS2	0.0173	0.0098	0.0053	4.37E-05	2.47E-05	1.12E-05
GSDS1	0.0163	0.0121	0.0087	4.21E-05	3.12E-05	2.20E-05
GSDSGDSS1	0.0164	0.0103	0.0043	4.18E-05	2.62E-05	1.11E-05
GDS1	0.0093	0.0074	0.0061	2.39E-05	1.90E-05	1.56E-05
GSD1	0.0289	0.0242	0.0021	6.49E-05	5.42E-05	5.39E-06
GDSS1	0.0251	0.0170	0.0048	6.05E-05	4.09E-05	1.07E-05
S1	0.0269	0.0231	0.0083	8.06E-05	6.92E-05	1.94E-05
D2	0.0098	0.0109	0.0073	3.08E-05	3.44E-05	2.18E-05
S2	0.0285	0.0128	0.0145	6.78E-05	3.04E-05	2.32E-05
D1	0.0189	0.0180	0.0145	5.02E-05	4.79E-05	4.17E-06
S3	0.0276	0.0236	0.0013	6.69E-05	5.70E-05	3.18E-06
S4	0.0258	0.0146	0.0192	6.58E-05	9.90E-05	1.45E-05
Average	0.0202	0.0149	0.0075	5.23E-05	4.27E-05	1.50E-05
Sum	0.3430	0.2539	0.1280	8.90E-04	7.30E-04	2.60E-04

Table 6. Results of Generalized Additive Model (GAM) analyses results on the effect of environmental factors on decomposition rates in fine mesh bags (k_{FM}), the effect of fauna metrics on decomposition in coarse mesh bags (k_{CM}) and on the difference between fine and coarse mesh (k_{CM}-k_{FM}). Table shows effective degrees of freedom (e.d.f), F and P significant (*) values and related variables with a P value minor than 0.1 (').

	e.d.f.	F	P-value
a) k_{FM}			
Channel Slope	2	1.372	0.2498
Channel Width	1	0.257	0.6128
Temperature	1	14.302	0.0002***
Temperature CV	1	2.884	0.0919'
Turbidity	2	2.391	0.0928'
Pfankuch	1	3.420	0.0543'
O2 Concentration	2	6.124	0.0019**
Discharge	1	9.293	0.0028**
Current Velocity	3	3.557	0.0183*
Dept CV	1	1.068	0.3033
b) k_{CM}			
Richness	1	1.473	0.2235
Abundance	6	2.656	0.0148*
Evenness	3	3.162	0.0190*
Fisher's Alpha	3	0.786	0.4901
c) k_{CM-FM}			
Richness	1	0.234	0.7103
Abundance	2	2.531	0.0591'
Evenness	4	4.096	0.0031**
Fisher's Alpha	2	0.918	0.4181

10. APPENDICES

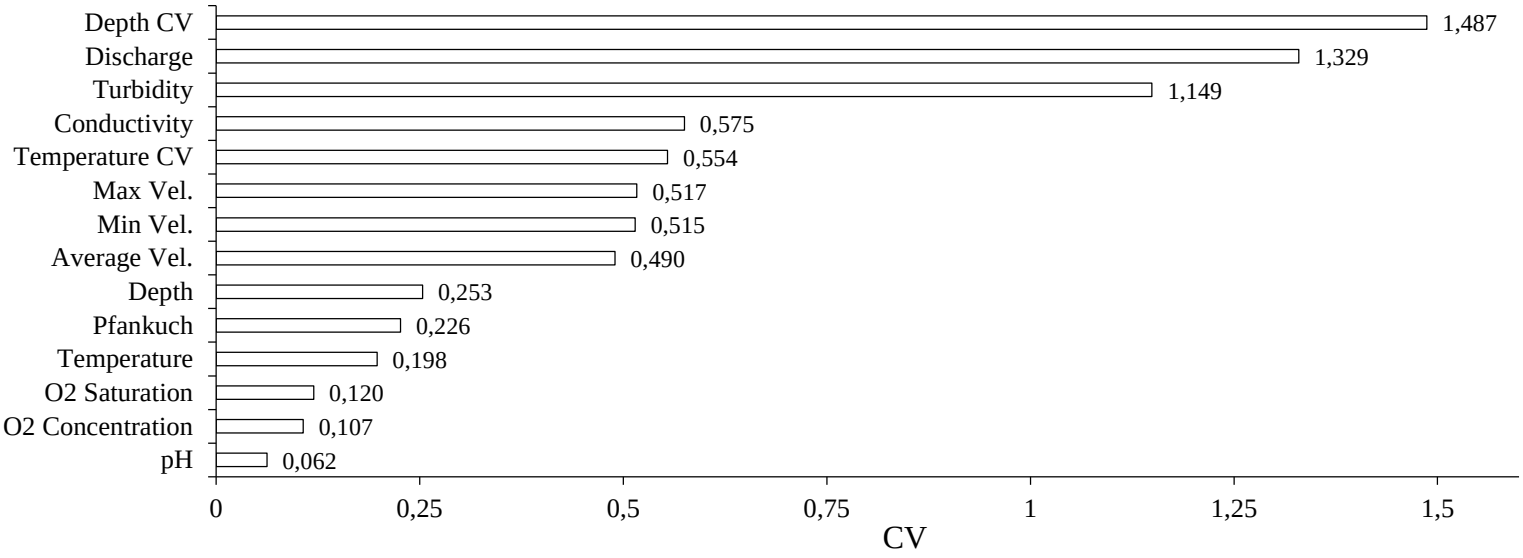
Appendix 1. Physical characteristics of the study sites.

Site	Altitude (m a.s.l.)	UTM X	UTM Y	Stream Order	Channel slope ($^0/_{00}$)	Channel width (m)	Average Temperature (°C)	Temperature CV	Turbidity (NTU)	Pfankuch	1/Pfankuch	Glaciality Index
G2	4109	811078	9943872	1	3.76	0.95	7.38	0.3259	284	23	0.0429	0.3282
G1	4195	811725	9945452	1	5.60	0.66	6.81	0.4178	144	22	0.0449	0.2968
GD2	4093	809927	9944126	2	3.00	0.88	8.07	0.2499	92	26	0.0382	0.2868
GS1	4105	811025	9943792	2	6.25	0.82	8.25	0.3684	103	25	0.0405	0.2839
GD1	4193	811710	9945398	2	5.20	0.91	7.04	0.2947	131	32	0.0313	0.2769
GDS2	4056	809793	9943234	2	6.38	1.00	8.75	0.1593	62	34	0.0294	0.2692
GSDS1	4042	809888	9943190	2	0.09	1.46	9.05	0.1483	95	28	0.0357	0.2678
GSDSGDSS1	4039	809661	9943130	3	5.38	2.50	8.08	0.2278	60	37	0.0270	0.2597
GDS1	4095	809877	9944066	2	3.00	0.87	8.65	0.1356	32	25	0.0400	0.2565
GSD1	4093	810941	9943760	2	2.00	1.15	8.15	0.2648	40	25	0.0397	0.2551
GDSS1	4050	809793	9943234	2	2.52	1.50	7.84	0.0751	17	30	0.0333	0.2304
S1	4090	809890	9944154	1	6.00	3.98	9.29	0.0479	10	40	0.0248	0.2023
D2	4108	811088	9943738	1	3.08	0.80	8.05	0.1876	6	38	0.0260	0.1740
S2	4101	811098	9943836	1	4.28	0.65	9.87	0.2603	7	42	0.0240	0.1719
D1	4202	811707	9945446	1	38.75	0.56	8.44	0.2167	4	33	0.0299	0.1616
S3	4045	809920	9943440	1	0.38	0.56	6.78	0.1056	3	34	0.0294	0.1598
S4	4050	809919	9943238	1	0.27	3.56	7.08	0.0002	1	39	0.0256	0.1292

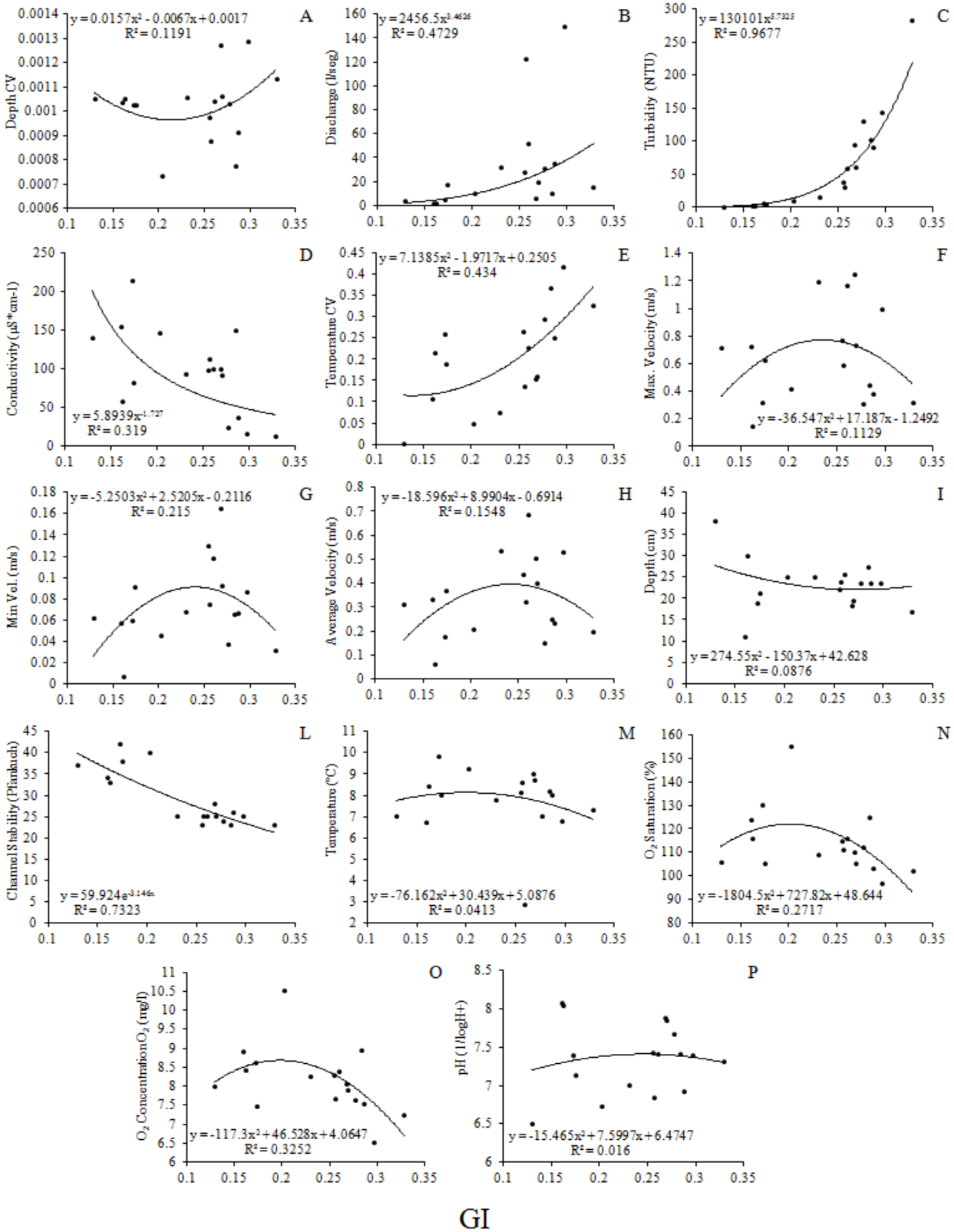
Appendix 2. Chemical and hydrological characteristics of the study sites.

Site	pH (1/logH+)	Conductivity (µS*cm-1)	O2 Saturation (%)	O2 Concentration (mg/l)	Discharge (l/s)	Average Vel. (m/s)	Maximum Vel. (m/s)	Minimum Vel. (m/s)	Depth (cm)	Depth CV
G2	7.31	12.2	102	7.24	15.3	0.196	0.323	0.032	16.89	0.00114
G1	7.39	15.2	97	6.51	149.5	0.528	1.000	0.086	23.76	0.00129
GD2	6.93	37.2	103	7.53	35.1	0.235	0.382	0.067	23.82	0.00091
GS1	7.42	149.8	125	8.94	9.7	0.251	0.444	0.065	27.43	0.00078
GD1	7.67	24.6	112	7.64	31.1	0.148	0.308	0.038	23.77	0.00103
GDS2	7.85	92.0	105	7.91	18.9	0.400	0.733	0.093	19.47	0.00106
GSDS1	7.89	100.5	110	8.07	5.9	0.505	1.250	0.165	18.29	0.00127
GSDSGDSS1	7.42	100.5	116	8.40	51.2	0.686	1.167	0.118	25.66	0.00104
GDS1	6.84	112.9	111	7.68	122.8	0.323	0.590	0.075	24.08	0.00088
GSD1	7.43	98.4	115	8.30	27.3	0.436	0.774	0.130	22.32	0.00098
GDSS1	7.01	93.0	109	8.25	31.9	0.533	1.200	0.068	25.11	0.00106
S1	6.74	147.1	155	10.52	10.0	0.205	0.422	0.045	25.26	0.00074
D2	7.14	81.5	105	7.46	17.5	0.371	0.625	0.091	21.48	0.00102
S2	7.40	214.4	130	8.61	4.4	0.179	0.323	0.059	19.15	0.00114
D1	8.05	58.6	116	8.41	1.3	0.062	0.153	0.007	30.28	0.00105
S3	8.08	154.0	124	8.90	1.5	0.333	0.729	0.058	11.09	0.00104
S4	6.51	140.6	106	8.01	3.7	0.313	0.714	0.063	38.38	0.00105

Appendix 3. Physicochemical variable's coefficient of variance along the GIG.



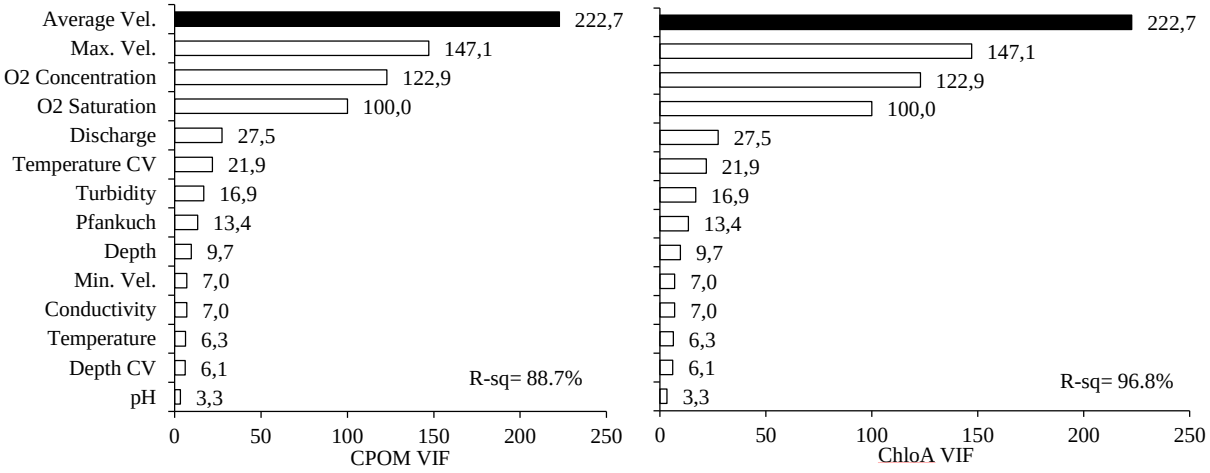
Appendix 4. GIG effect over each physicochemical variable.



Appendix 5. Linear correlation table for chemical and hydrological variables.

	Channel slope	Channel width	Average Temperature	Temperature CV	Turbidity	1/Pfankuch	pH	Conductivity	O2 Saturation	O2 Concentration	Discharge	Average Vel.	Maximum Vel.	Minimum Vel.	Depth	Depth CV
Channel slope	0	0.4510	0.5730	0.5865	0.5871	0.6792	0.1294	0.4335	0.7399	0.7052	0.6388	0.0749	0.0780	0.0401	0.2237	0.9099
Channel width	-0.1960	0	0.6822	0.0104	0.3266	0.0725	0.0151	0.2671	0.0856	0.0352	0.4789	0.5447	0.4438	0.8083	0.0359	0.2306
Average Temperature	0.1472	0.1072	0	0.5310	0.1964	0.2368	0.9133	0.0367	0.0382	0.0539	0.3560	0.6014	0.6203	0.4659	0.8168	0.3761
Temperature CV	0.1421	-0.6028	-0.1634	0	0.0051	0.0103	0.2107	0.0743	0.2704	0.0626	0.1823	0.7843	0.3956	0.9122	0.4599	0.3978
Turbidity	-0.1419	-0.2533	-0.3296	0.6464	0	0.0034	0.6653	0.0049	0.1011	0.0405	0.4227	0.8498	0.7054	0.8258	0.3183	0.2498
1/Pfankuch	-0.1082	-0.4464	-0.3032	0.6035	0.6680	0	0.9150	0.0268	0.0595	0.0338	0.0246	0.6568	0.7476	0.5966	0.5748	0.6307
pH	0.3828	-0.5778	-0.0286	0.3199	0.1132	0.0280	0	0.6755	0.8322	0.8889	0.3903	0.9373	0.9336	0.7363	0.0303	0.1034
Conductivity	-0.2035	0.2853	0.5096	-0.4438	-0.6479	-0.5354	-0.1096	0	0.0038	0.0022	0.1381	0.9118	0.9335	0.7065	0.9969	0.2334
O2 Saturation	0.0870	0.4291	0.5060	-0.2834	-0.4112	-0.4659	-0.0556	0.6620	0	0.0000	0.1390	0.2321	0.2876	0.4061	0.8976	0.0167
O2 Concentration	0.0991	0.5131	0.4752	-0.4610	-0.5010	-0.5166	-0.0367	0.6896	0.9402	0	0.0275	0.4251	0.5766	0.5910	0.8568	0.0099
Discharge	-0.1228	-0.1843	-0.2388	0.3396	0.2082	0.5421	-0.2227	-0.3749	-0.3742	-0.5332	0	0.1289	0.2798	0.5464	0.8470	0.5285
Average Vel.	-0.4431	0.1580	-0.1365	-0.0718	-0.0497	0.1162	-0.0207	-0.0291	-0.3061	-0.2071	0.3833	0	0.0000	0.0002	0.7281	0.1777
Maximum Vel.	-0.4388	0.1990	-0.1295	-0.2203	-0.0990	0.0843	0.0219	0.0219	-0.2738	-0.1458	0.2781	0.9506	0	0.0003	0.7489	0.0915
Minimum Vel.	-0.5020	0.0636	0.1897	-0.0290	-0.0577	0.1383	0.0882	0.0986	-0.2155	-0.1404	0.1573	0.7797	0.7688	0	0.4320	0.2505
Depth	0.3114	0.5114	-0.0607	-0.1922	-0.2576	-0.1465	-0.5254	0.0010	-0.0338	0.0474	0.0506	-0.0911	-0.0839	-0.2041	0	0.2995
Depth CV	-0.0297	-0.3070	-0.2292	0.2193	0.2954	0.1257	0.4086	-0.3053	-0.5708	-0.6064	0.1644	0.3430	0.4221	0.2949	-0.2674	0

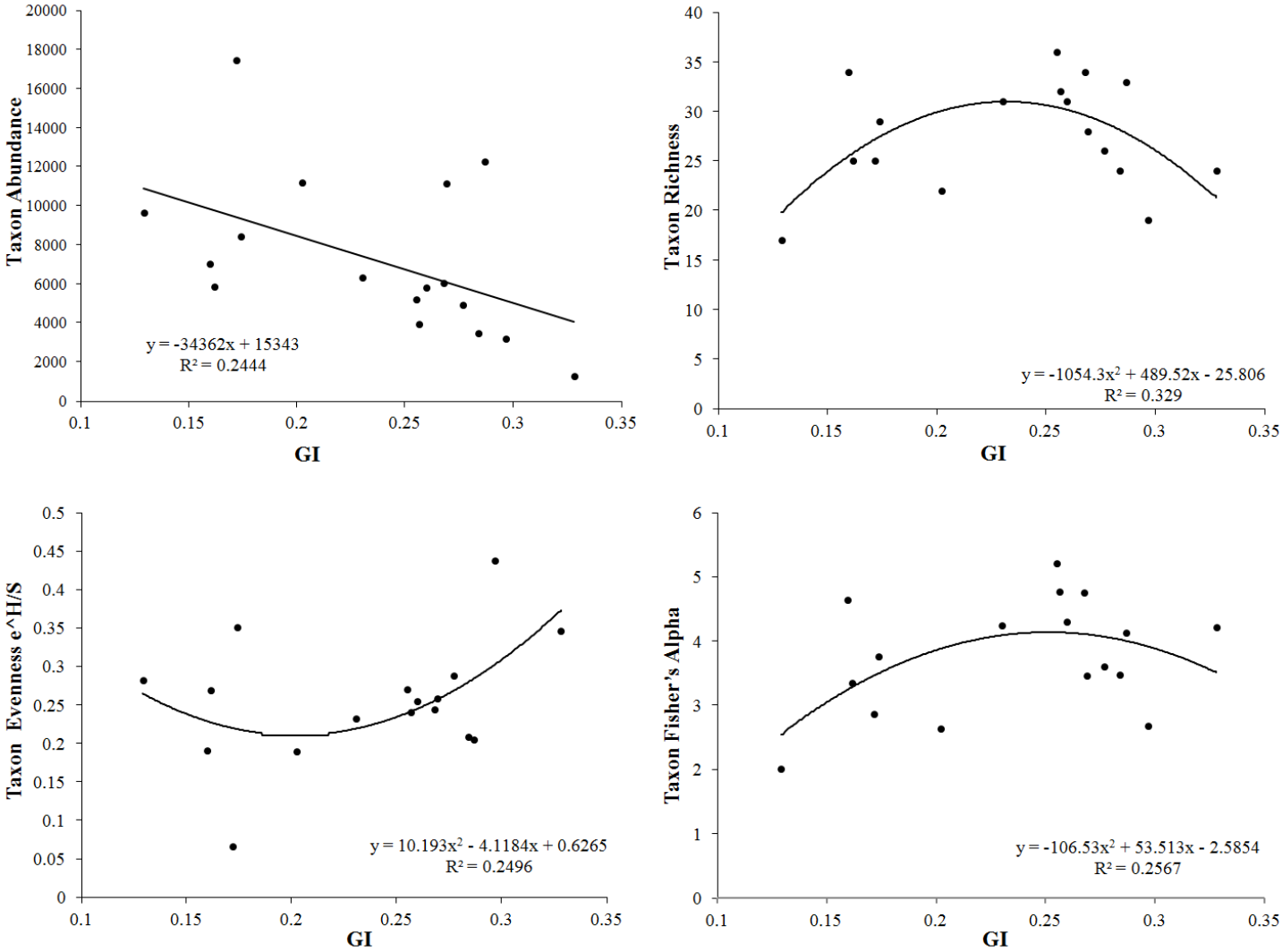
Appendix 6. Variation inflation factor (VIF) from linear regression analysis of primary food sources (PFSs) for each physicochemical variable; black bar denotes most related factor in PFSs distribution.



Appendix 7. Taxon abundance from benthic samples (m^2)

Site	G2	G1	GD2	GS1	GD1	GDS2	GSDS1	GSDSGDSS1	GDS1	GSD1	GDSS1	S1	D2	S2	D1	S3	S4	Sum	Average	%
Sphaeriidae	0	0	0	0	4	0	12	0	0	0	8	12	8	4	0	8	0	56	3	0.05
Naididae	38	47	91	40	50	58	26	243	53	50	65	72	81	67	68	29	32	1110	65	0.92
Lumbriculidae	28	668	96	28	532	416	20	132	240	8	24	20	16	200	296	24	32	2780	164	2.31
Hirudinea	0	0	0	0	4	0	4	40	0	8	0	4	0	44	192	4	0	300	18	0.25
Neoelmis sp. (L)	0	0	0	0	4	0	4	40	0	8	0	4	0	48	192	4	0	304	18	0.25
Neoelmis sp. (A)	0	0	0	0	8	0	8	80	0	16	0	8	0	92	384	8	0	604	36	0.50
Prionocyphon sp.	4	28	48	40	20	108	20	64	84	76	0	16	0	0	48	4	0	560	33	0.47
Blepharicera sp.	0	0	8	4	0	24	44	116	0	52	0	0	4	0	0	0	0	252	15	0.21
Alluaudomyia sp.	52	692	668	120	1476	980	28	84	104	216	8	0	84	12	20	12	0	4556	268	3.79
Chironomidae	732	536	4544	300	1328	3476	2812	2940	1376	1780	1692	1156	992	140	2416	2872	2184	31276	1840	25.99
Chelifera sp.	0	12	128	12	56	4	136	76	16	4	124	12	52	0	0	20	96	748	44	0.62
Hemerodromia sp.	0	0	0	0	0	0	4	0	0	0	0	0	0	0	20	0	0	24	1	0.02
Molophilus sp.	0	0	480	0	8	116	28	40	104	24	4	4	92	0	0	40	0	940	55	0.78
Limnophora sp.	4	8	64	0	4	0	4	0	8	24	4	8	4	56	0	32	0	220	13	0.18
Simulium sp.	124	240	316	44	196	404	80	72	116	12	96	104	4	132	52	304	0	2296	135	1.91
Andesiops sp.	68	660	5236	208	756	4584	700	892	1416	448	2744	2072	1740	388	112	692	4340	27056	1592	22.49
Claudioperla sp.	0	12	104	4	64	236	4	0	16	12	16	0	4	0	0	4	12	488	29	0.41
Mortoniella sp.	4	0	0	8	0	20	1108	112	8	0	56	8	572	28	0	56	0	1980	116	1.65
Atopsyche sp.	16	36	52	24	28	32	20	0	0	28	20	0	36	12	144	4	80	532	31	0.44
Cailloma sp.	24	12	180	0	12	0	60	16	4	8	56	0	72	0	28	4	8	484	28	0.40
Neotrichia sp.	0	0	0	28	0	0	12	24	4	92	324	0	68	0	0	72	28	652	38	0.54
Ochrotrichia sp.	0	0	0	24	0	0	12	240	0	336	324	0	352	0	0	72	28	1388	82	1.15
Anomalocosmoecus sp.	0	0	44	0	0	0	488	360	16	112	412	764	1832	0	0	904	1460	6392	376	5.31
Hyallela sp.	0	8	56	2100	36	44	144	180	260	1004	128	6484	1144	15972	1896	1400	596	31452	1850	26.14
Ostracoda	0	0	0	20	8	0	0	12	8	24	20	116	24	104	384	0	0	720	42	0.60
Planariidae	16	84	12	280	32	104	8	8	16	484	72	92	544	212	4	396	640	3004	177	2.50
Nematoda	20	0	4	4	0	8	44	0	8	4	8	0	12	4	20	8	8	152	9	0.13

Appendix 8. GIG effect over each ecological variable.



Appendix 9. Functional feeding group (FFG) abundance from benthic samples (m^2).

Site	GF-2	GF-1	1J-3	1J-2	1J-1	2J-3	3J-2	3J-3	2J-1	2J-2	3J-1	SP-1	SD-2	SP-2	SD-1	SP-3	SP-4	Sum	%	Average
Predators/Scrapers	52	692	668	120	1476	980	32	84	104	216	8	0	84	12	40	12	0	4580	3.81	269
Predators/Collectors	40	48	232	24	40	32	80	16	4	36	76	0	108	12	172	8	88	1016	0.84	60
Predators	40	104	208	296	96	116	196	124	48	524	208	116	612	316	216	460	744	4424	3.68	260
Scrapers	72	660	5724	220	764	4744	1880	1160	1528	524	2804	2084	2408	416	112	788	4340	30228	25.12	1778
Shredders/Scrapers	0	8	56	2100	40	44	148	220	260	1012	128	6488	1144	16020	2088	1404	596	31756	26.39	1868
Shredders	0	12	148	56	64	236	516	624	36	552	1076	764	2256	0	0	1052	1528	8920	7.41	525
Shredders/Collectors	4	28	48	40	28	108	28	144	84	92	0	24	0	92	432	12	0	1164	0.97	68
Collectors/Scrapers	798	1251	4731	368	1910	3950	2858	3315	1669	1838	1781	1248	1089	407	2780	2925	2248	35166	29.23	2069
Collectors	124	240	316	64	208	404	92	84	124	36	124	232	36	240	436	312	0	3072	2.55	181